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Grouping dynamics of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Amazonian Ecuador

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Grouping dynamics of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Amazonian Ecuador

by

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Dedication

To my parents, David and Terri, who have provided me with unconditional love and support.

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Abstract

Grouping dynamics of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Amazonian Ecuador

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Predator avoidance, resource distribution, and reproductive strategies all play a crucial role in shaping the social structure of animal societies. The fission-fusion dynamics of some animal societies – where core social units are able to break apart or coalesce into parties of variable size and composition – can allow individuals to mediate the cost-benefit tradeoffs of varying party size according to particular environmental or social conditions. Here, I couple ecological, behavioral, and spatial data with molecular genetic methods and analytical techniques (Social Network Analysis) to examine spatiotemporal association patterns among woolly monkeys from four social groups at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador. The woolly monkeys in this populations demonstrated relatively high degrees of fission-fusion dynamics, with groups dividing frequently into subgroups and showing temporally variable cohesion among group members. I found no evidence, however, that subgroups consistently and repeatedly comprised the same sets of individuals. Spatial associations and social interactions were not limited to members of a single social group, and tolerant associations between members of some social groups occurred with relatively high frequency. Genetic analyses revealed no difference in the average relatedness of male and female same-sex dyads, although, adult males tended to have more close relatives both within and between social groups than adult females. Regardless of sex, animals were no more likely to associate with genetic relatives than with to non-relatives. This study also corroborated earlier suggestions that woolly monkeys exhibit some degree of bisexual dispersal, with some males leaving their natal group, in contrast to the pattern that characterizes closely related species of primates. Genetic data also suggest that woolly monkeys live in a dispersed network of kin, where both males and females had first order relatives in neighboring groups. Kinship ties among animals in different groups may play a role in facilitating tolerant mixed group associations, which are common in the study population. As observed in other studies, home range overlap between neighboring groups was extensive, with particular pairs of groups showing higher degrees of overlap than others. Finally, woolly monkeys demonstrated strong reproductive seasonality, with births and conceptions confined to a few months out of the year. My finding that seasonal variation in group cohesion and ranging patterns was not related to fruit availability, but did covary with a behavioral index of mating opportunities, suggest that grouping and ranging dynamics in woolly monkeys may not primarily be driven by competition over food, but rather by competition over mates.

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Chapter 1: Introduction

BACKGROUND

Predator avoidance, resource distribution, and reproductive strategies all play a crucial role in shaping the social structure of animal societies (Alexander 1974; Isbell and Young 2002; Rubenstein and Wrangham 1986). The fission-fusion dynamics of some animal societies – where social groups are able to fission or coalesce into parties of variable size and composition – can allow individuals to mediate the cost-benefit tradeoffs of varying party size according to particular environmental or social conditions (Aureli et al. 2008; Chapman and Chapman 2000; Klein and Klein 1977; Lehmann and Boesch 2004; Symington 1990). Individuals belonging to social groups that show high levels of fission-fusion dynamics may form larger aggregations when reproductive, foraging, or antipredator benefits are possible, but may also dissolve into smaller subsets of individuals, or subgroups, once intragroup competition exceeds those benefits.

Historically, group-living primates were characterized as those living in socially cohesive groups versus those with the fluid and flexible association patterns of fission-fusion (Kappeler and van Schaik 2002; Kummer 1971). This modal categorization recognized only a handful of primate species that displayed the most extreme forms of flexible association patterns as living in "fission-fusion" societies, obscuring the fact that many taxa show more intermediate levels of spatiotemporal cohesion among groupmates (Aureli et al. 2008; Di Fiore and Strier 2004; Strier 1989). As a result, much of our understanding of the ecological and social factors influencing fission-fusion dynamics in primate societies comes from studies of chimpanzees (e.g., Boesch and Boesch-Achermann 2000; Goodall 1986; Langergraber et al. 2007; Lehmann and Boesch 2004; Mitani et al. 2002; R. W. Wrangham 1977), spider monkeys (e.g., Chapman 1990;

Chapman et al. 1995; Link et al. 2011; Shimooka 2003; Symington 1987; Symington 1988), geladas (e.g., Dunbar and Dunbar 1975; Dunbar 1993; Dunbar 1984; Kawai et al. 1983), and hamadryas baboons (e.g., Kummer 1968, 1971; Schreier and Swedell 2009; Swedell 2011; Swedell and Plummer 2012), which manifest distinct forms of fission-fusion association patterns. Spider monkeys and chimpanzees are classically described as showing "individualistic" fission-fusion patterns, where animals break apart and coalesce with different members of their community over the course of a day, producing association patterns that are highly variable over time (Lehmann and Boesch 2004). By contrast, geladas and hamadryas baboons live in modular, multi-tiered societies and show a "molecular" pattern of fission-fusion associations in which the smallest social unit has stable group membership and where units may fuse at different points in time into successive different hierarchical levels (e.g., one-male units join with other one-male units to form teams [geladas; Grueter et al. 2012; Snyder-Mackler et al. 2012] or bands [hamadryas baboons; Swedell 2011]; bands may fuse into clans, and clans into troops).

As observations on animals societies have accumulated, researchers have come to appreciate that flexible fission-fusion grouping patterns among primates and other vertebrates are more widespread and more complex than previously recognized (Aureli et al. 2008; Kinzey and Cunningham 1994). Animal societies currently considered to demonstrate high levels of fission-fusion dynamics include, but are not limited to elephants (e.g., Wittemyer et al. 2005), social carnivores (e.g. Holekamp et al. 1997), cetaceans (e.g. Connor et al. 2000), equids (e.g. Rubenstein et al. 2015; Sundaresan et al. 2007), even-toed ungulates (e.g., Bercovitch and Berry 2013; Fortin et al. 2009), bats (e.g., Kerth et al. 2006, 2011), birds (e.g., Aplin et al. 2012), and some fish (e.g. Croft et al 2003). Among primates, high levels of fission-fusion dynamics have been identified not only in spider monkeys, chimpanzees, geladas, and hamadryas baboons, but have also been observed to varying degrees in brown lemurs (Overdorff et al. 2003; Toborowsky 2008), black-and-white ruffed lemurs (Holmes et al. 2016; Baden et al. 2016), mouse lemurs (Radespiel et al. 2001), capuchins (Lynch-Alfaro 2007), howler monkeys (Bezanson et al. 2008), muriquis (Coles et al. 2012; Dias and Strier 2003), woolly monkeys (Di Fiore et al. 2011), uakaris (Bowler et al. 2012), guinea baboons (Patzelt et al. 2014), macaques (Fukuda 1989; Menard 2002), mangabeys (Dolado et al. 2016), snub-nosed monkeys (Ren et al. 2012), orangutans (van Schaik 1999), and modern humans following traditional subsistence strategies (Marlowe 2005).

Considering the varying degrees of spatiotemporal cohesion among animal societies, Aureli and colleagues (2008) put forth a seminal paper outlining a new framework to better characterize, and thus compare, fission-fusion dynamics across and within taxa. In this multidimensional framework, the degree of fission-fusion dynamics can be characterized along three major dimensions: temporal variation in spatial cohesion, temporal variation in party size, and temporal variation in party composition. Species may show little temporal variation among these three dimensions (e.g., howler monkeys), some may show high degrees in one or two of these dimensions (e.g. hamadryas baboons), or some may show high variation in all three dimensions (e.g., spider monkeys). Given that variation in spatiotemporal cohesion of animal groups plays an important role in allowing animals to adapt to fluctuations in their social and ecological environments (Strier 1989), understanding patterns of fission-fusion dynamics across and within taxa is important for understanding how social, ecological, demographic, and genetic factors influencing variation in and maintenance of sociality (Aureli et al. 2008).

While the precise factors influencing dynamic grouping patterns are not entirely clear, we find, generally, that adjustments to group size often occur in response to feeding competition, social factors (including reproductive strategies), demographic conditions, and predation risk. In terms of feeding competition, changes in subgroup size and cohesion are often, but not always, tied to food availability, particularly when preferred foods are patchily distributed in space and time, like fruit (Chapman et al. 1995; Symington 1987, 1988). When preferred food is abundant, within-group feeding competition is relaxed, allowing for larger, more cohesive subgroups (e.g., Asensio et al. 2009; Chapman et al. 1995; Coles et al. 2012). However, as food resources become scarce, intragroup feeding competition increases, forcing individuals to spread out and either forage on their own or in smaller subgroups (e.g., Anderson et al 2002; Klein and Klein 1977; Wrangham 1980, 1986; Schrier and Swedell 2012). Given that larger groups must commonly travel farther per day to compensate for faster depletion rates than smaller groups, reducing subgroup size may also reflect a strategy to reduce overall relative ranging costs and time spent traveling (Asensio et al. 2009; Chapman et al. 1995; Chapman and Chapman 2000; Dunbar 1988; Janson and Goldsmith 1995; Korstjens et al. 2006).

In long-term studies, fission-fusion dynamics also have been noted to fluctuate with changes in demography. For example, smaller community sizes are associated with increased cohesion and subgroup size (Dias and Strier 2003; Lehmann and Boesch 2004). Social factors thought to influence variation in subgroup size include cooperative hunting (Boesch and Boesch 1989; Pearson 2009), territorial patrols (Wallace 2008), the socialization of infants (Chapman et al. 1994; Williams et al. 2002), and female reproductive status (Anderson et al. 2002, Boesch and Boesch-Achermann 2000; Chapman 1990; Goodall 1986; Hashimoto et al. 2001; Matsumoto-Oda et al. 1998; Mitani et al. 2002; Shimooka 2003; Symington 1987; Wrangham 2000). For example, mixed-sex subgroups in both spider monkeys and chimpanzees tend to be larger when estrus or cycling females are present (Anderson et al. 2002; Boesch and Boesch-Achermann

2000; Chapman 1990; Goodall 1986; Hashimoto et al. 2001; Matsumoto-Oda et al. 1998; Mitani et al. 2002; Shimooka 2003; Symington 1987; Wrangham 2000), while females that are either pregnant or lactating tend to be less social and spend more time alone or in small subgroups with other lactating females (Goodall 1986; Matsumoto-Oda et al. 2008; Nishida 1990; Sakura 1994, Wrangham and Smuts 1980).

One of the strongest factors thought to influence primate behavior and sociality is predation pressure (Alexander 1974; van Schaik 1983), with the formation of groups thought to provide a variety of benefits, including reducing individual predation risk through dilution and enhancing predator detection and cooperative defense. Many species characterized by higher levels of fission-fusion dynamics tend to be large bodied and likely experience lower predation rates compared to those showing lower fission-fusion dynamics (Lehmann et al. 2007). However, there are several species in which predation risk has been identified to be a predictor of subgroup size. For these species, the threat of predation is often predictable in time or space allowing animals to react accordingly, such as the aggregation of hamadryas baboons around communal sleeping cliffs (Schrier and Swedell 2012) or the increase in spider monkey subgroup size when visiting terrestrial mineral licks (Link and Di Fiore 2013).

In conjunction with the factors listed above, grouping dynamics may also reflect preferential associations between individuals based on their attributes, such as genetic relatedness. Across mammals, kinship is considered to play a crucial role in shaping social structure, provided that individuals that associate with kin receive indirect fitness benefits (Hamilton 1964; Chapais and Berman 2004; Silk 2009; Langergraber 2012). The ability to interact with kin, however, will be largely dependent on a species' dispersal pattern (Di Fiore 2012). For animals with sex-biased dispersal, individuals that remain in their natal group will often have access to an extended network of genetic relatives with whom they may form strong and enduring social bonds or coalitions with (Silk 2009; Langergraber 2012). Although animals that disperse from their natal group often leave genetic relatives behind, some may maintain long-term associations with kin by immigrating into groups to which other relatives have previously dispersed, through parallel dispersal (reviewed in Langergraber 2012), or by residing in neighboring groups with intermittent contact (Bradley et al. 2004).

ORGANIZATION OF THE DISSERTATION

In this dissertation, I investigate the factors influencing the grouping dynamics of lowland woolly monkeys, a taxon that has been described as living in relatively cohesive groups that nonetheless show some propensity for fluid and flexible association patterns (reviewed in Di Fiore et al. 2011). More specifically, I examine how range use and spatiotemporal association patterns within and between animals living in multiple social groups of woolly monkeys at the Tiputini Biodiversity Station, Ecuador are related to possible reproductive opportunities, habitat wide fruit availability, and genetic relatedness. In doing so, I also explore how dyadic association patterns scale up to the observed social structure and evaluate whether woolly monkeys live in “molecular” societies comprising more than one tier of organization. Given that most of our understanding of fission-fusion social dynamics comes from studies of taxa that show the most extreme flexibility in spatiotemporal association patterns, the data presented here provide a critical comparative dataset to better understand the range of fission-fusion dynamics found in mammals and to better evaluate the various behavioral strategies animals may employ to balance the costs/benefits of group living.

The dissertation is presented in the form of three independent (though interrelated) manuscripts, each formatted for submission to a journal or edited volume with specific objectives, methods, results, and interpretation. Below, I summarize the focus of each chapter and the logic tying them together.

Because female reproductive status is expected to play an integral role in the patterning of spatiotemporal associations in fission-fusion taxa, I begin this dissertation by evaluating, in **Chapter 2**, the degree of reproductive seasonality (i.e., how clustered reproductive events such as births and conceptions were in time) seen at our site in both woolly monkeys and spider monkeys, a closely-related taxon. For this chapter, I incorporate long-term demography data collected under the supervision of Andres Link, Anthony Di Fiore, and myself on four groups of woolly monkeys between 2013 and 2016 and one group of spider monkeys between 2006 and 2016. The timing and frequency of copulations, births, and conceptions are compared to an index of variation in the abundance of ripe, fleshy fruits (a preferred resource for both taxa) to test several predictions suggested based on the income-capital breeding framework of primate female reproductive strategies (Brockman and van Schaik 2005; Di Bitetti and Janson 2000; Janson and Verdolin 2005). The results from this chapter allow me to make better predictions regarding the effects of mating opportunities on the association and ranging patterns of woolly monkeys in subsequent chapters. At the time of completion of this dissertation, this chapter had been submitted to and reviewed at the *American Journal of Primatology*, and a revised version addressing the reviewer comments is currently in progress.

In **Chapter 3** of this dissertation, I examine the fission-fusion dynamics and ranging patterns of four social groups of woolly monkeys in relation to both fruit availability and mating opportunities. For this chapter, I use a combination of location data, group association records, and observations of mating behavior collected simultaneously by myself and several field assistants between August 2014 and December 2015. Although several previous studies had investigated the influence of fruit availability on woolly monkey ranging patterns, they typically did not incorporate simultaneous observers and thus yielded less precise data on temporal variability in association patterns, spatial cohesion, and concurrent space use and on intergroup dynamics. Additionally, these earlier studies did not consider simultaneously the importance of both fruit availability and mating opportunities on grouping patterns. In this chapter, I present basic data on the percent of time that woolly social groups spent divided into subgroups, on variation in subgroup size, and on spatial cohesion within and between subgroups as reflected by interindividual distances between simultaneously-followed focal individuals. I also characterize ranging patterns and space use of each of the four social groups, presenting data on daily path length, home range size, core area size, and degree of home range overlap. I compare rates of intergroup encounters to indices of home range overlap between different social groups to determine if intergroup encounters occurred more or less often than expected by chance. Finally, I also explore how patterns of group cohesion, subgroup size, and ranging behavior relate to temporal fluctuations in both habitat wide estimates of ripe fruit availability and the availability of mating opportunities. At the time of completion of this dissertation, a version of this chapter has been accepted for publication as a chapter in an edited volume titled *Movement Ecology of Neotropical Forest Mammals*.

In **Chapter 4**, I apply social network analysis to data on association patterns and interindividual proximity collected during focal follows of individually-recognized animals from four social groups to better characterize and understand the flexible social structure of woolly monkeys. I also use data on genetic relatedness among the same set of individuals to explore how patterns of kinship map onto and influence patterns of social association. Although woolly monkeys are often considered a male-philopatric taxon, prior genetic work on this population has suggested that males may also disperse to some degree and that adult animals of both sexes may have close genetic relatives residing in their own social group and/or in neighboring social groups as well (Di Fiore et al. 2009). The behavioral data used for this chapter came from two four-month subsets of field data collected on individually recognized woolly monkeys by myself and several assistants. These periods corresponded to two different epochs in the annual reproductive cycle of woolly monkeys at the site: the 'breeding season' (August to November 2014), when mating is common and most conceptions occur, and the 'birth season' (May to August 2015), when many females either gave birth or were approaching parturition. Social structure was evaluated for each of these periods using hierarchical cluster analysis and by considering the modularity of the social networks implied by association patterns and interindividual proximity scores. Genetic data were based on DNA extracted from either feces or tissue samples collected between 2013 and 2017. Individuals were genotyped at a panel of 12 variable microsatellite markers, and these genotypes were used to estimate pairwise relatedness among all animals in the population.

Finally, in **Chapter 5** I summarize the major findings of my research, discuss woolly monkey fission-fusion dynamics in comparison to other taxa, acknowledge some of the limitations of this project, and highlight important areas for future research.

Chapter 2: Reproductive seasonality in two sympatric primates (*Ateles belzebuth* and *Lagothrix lagotricha poeppigii*) from Amazonian Ecuador

INTRODUCTION

Most wild populations of primates demonstrate some degree of reproductive seasonality (Di Bitetti and Janson 2000; Janson and Verdolin 2005; Lancaster and Lee 1965; Lindburg 1987). The strength of seasonality, i.e. how clustered reproductive events are in time, is often correlated with the degree of environmental fluctuation, most notably in rainfall and food availability. This pattern arises, in part, because the optimal timing of conceptions and births is likely to be dependent on the balance between food availability and the energetic and nutritional demands of mothers and infants during gestation, lactation, and weaning (Crockett and Rudran 1987; van Schaik and van Nordwijk 1985).The timing of reproductive events in relation to food availability has been frequently characterized using the income-capital breeding framework (Brockman and van Schaik 2005; Carnegie et al. 2011; Di Bitetti and Janson 2000; Janson and Verdolin 2005; Lewis and Kappeler 2005a, 2005b; Richard et al. 2000). The framework was originally created to describe reproductive strategies for increasing clutch size in birds (Drent and Daan 1980), but was later reworked by life-history theorists (Jönsson 1997; Stearns 1989, 1992) to focus on tactics that cover the whole reproductive cycle, not just the production of additional offspring (Brockman and van Schaik 2005). In its current form, the model can be viewed as a continuum of solutions differentiated by the degree to which an organism relies on stored energy to finance reproductive costs (Jönsson 1997; Stephens et al. 2009). Marking the extreme ends of the continuum, an "income" breeder is one that uses current food intake to initiate reproductive events (mating, conception, and the onset of gestation), whereas a “capital” breeder builds and stores energy reserves to draw from during later phases of reproduction (maintenance of pregnancy, lactation) (Stearns 1992). Although few species are purely income or capital breeders, testing predictions about the timing and frequency of reproductive events in relation to seasonally fluctuating resources may allow classification of individuals as more representative of one strategy than the other (Brockman and van Schaik 2005; Stephens et al. 2009).

Among non-human primates, three main reproductive patterns have been suggested (Table 2.1; Brockman and van Schaik 2005; Janson and Verdolin 2005). Income-I breeders, also known as “classic breeders,” are generally smaller bodied species (e.g., those <3 kg), with shorter life spans, that rely on high quality, seasonal resources like fruits and insects. Their reproductive responses are predicted to include: 1) a conception window heavily influenced by exogeneous factors, such as photoperiod or rainfall, 2) little to no fat accumulation during pregnancy, 3) low prenatal mortality rates, and 4) little to no interranual variation in birth rates, but 5) high interannual variation in infant mortality rates (Brockman and van Schaik 2005). They generally reproduce once per year, and often show a narrow birth peak with births timed such that weaning occurs during peak food availability (Brockman and van Schaik 2005; Janson and Verdolin 2005). In doing so, Income-I breeders are thought to improve infant survival by reducing the energetic stress that infants experience during weaning (Altmann 1980; Crockett and Rudran 1987). Infant survivorship, is therefore, predicted to be higher for infants born during the birth window that permits weaning to occur during periods of greatest food availability compared to infants born outside of it (Di Bitetti and Janson 2000).

Finally, for primates living in environments with unpredictable peaks in food availability, or for those with relatively long interbirth intervals, the timing of reproductive events may be dependent principally on maternal body condition needed to support cycling and maintain gestation rather than on food availability at either the time of infant weaning or of peak lactational stress for mothers. Such females are considered “capital” breeders, as they follow a strategy of accumulating and storing energy reserves for future reproductive events such as gestation and lactation (Stearns 1992; van Schaik and van Noordwijk 1985). The reproductive responses of strictly capital breeders are predicted to include: 1) a variable conception window that is cued endogenously through individual condition thresholds or energy balance, 2) accumulation of fat reserves throughout pregnancy, 3) high prenatal mortality rates, 4) high interannual variation in birth rates, and 5) low variation in infant mortality rates (Brockman and van Schaik 2005). If capital breeders mate throughout the period of increasing food availability but only conceive once their body condition reaches an adequate threshold, then their births are predicted to occur after the mean peak in food abundance by a period of time equal to the delay in conception plus gestation length (Janson and Verdolin 2005).

In an influential review of the timing of births in platyrrhines, Di Bitetti and Janson (2000) found that, across species, births tend to occur before the peak in food availability. They argue that, for small-bodied species, this pattern would allow peak lactation to occur during peak food availability (i.e., that small-bodied species are Income-II breeders), while for larger species it would allow weaning of offspring to occur before the start of the lean season (Income-I breeder). However, the atelins, which are the largest of the New World primates, do not neatly conform to this pattern. Instead, despite living in climactically different environments, atelins tend to give birth when preferred resources, such as new leaves for muriquis (*Brachyteles arachnoides*) and ripe fruits for woolly monkeys (*Lagothrix spp.*) and spider monkeys (*Ateles spp.*), are relatively scarce (Nishimura 2003). Given their large body size and long period of infant dependency, too, it is unlikely that atelins are strict income breeders, but rather fall towards the other end of the income-capital breeding continuum – unable to conceive and successfully gestate until they reach an adequate body condition (Nishimura 2003; Strier 1996a, Strier and Ziegler 1997; Strier et al. 2003).

Observational data, coupled with physiological data, support the notion that atelin primates may be capital breeders. For example, in spider monkeys and woolly monkeys, copulations are observed year-round, yet births are reported to only occur during 8-9 months out of the year in spider monkeys (Shimooka et al. 2008) and during 6 months out of the year in woolly monkeys (Nishimura 2003). Among muriquis, matings are rarely observed during the dry season, when preferred resources are scarce. Thus, if a female muriqui fails to conceive by the end of the wet season, when preferred resources are abundant, she will potentially experience a full year delay in reproduction, waiting until the next rainy season to recommence sexual activity (Strier 1996a). Despite having such a narrow conception window (> 65% of conceptions occur November-February), muriqui males do not exhibit the testicular recrudescence typical of seasonal breeders, nor do they show variation in fecal testosterone concentrations across the year, supporting the notion that female reproductive success is dependent on female body condition (Strier 1996a). Furthermore, Strier and colleagues (2003) have suggested that female muriquis may undergo physiological changes related to pre-breeding fat storage, evidenced by increased cortisol levels prior to the mating season in females but not in males. Finally, all multiparous atelins exhibit several months of ovarian cycling before conception is achieved, suggesting that maternal body condition may be critical for successful conception. The average delay from resumption of cycling to conception is around 7 months for woolly monkeys (Nishimura, 2003) and 3-6 cycles for spider monkeys (Campbell et al. 2001) and muriquis (Strier and Ziegler 1997; but see Strier et al. 2003).

While together this set of observations strongly suggests that atelins are capital breeders, few studies to date have examined whether and how reproductive behavior and births are related to temporal variation in resource availability at a given site over the long term. In this paper, we aim to fill this gap by presenting long-term data on the timing of reproductive events for two sympatric atelin primates – white-bellied spider monkeys (*Ateles belzebuth*) and lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) – at the Tiputini Biodiversity Station (TBS) in

Amazonian Ecuador. Specifically, we present data on the distribution of observed copulations, inferred months of conception, and births in both species over multiple years and examine how these are related to seasonal patterns of ripe fruit availability at the site. We also present data on animals' return to sexual activity post-parturition and on inter-annual variation in birth sex ratios. Placed within a comparative context, these data enhance our understanding of atelin reproductive strategies and sexual behavior.

Spider monkeys and woolly monkeys are highly frugivorous primates, preferring ripe fruit and supplementing their diet with young leaves, shoots, and flowers (Cant 1990; Chapman 1987, 1988; Defler and Defler 1996; Dew 2005; Di Fiore 2004; Klein and Klein 1977; Peres 1994; van Roosmalen 1985; Stevenson 1992, Stevenson et al. 1994; Symington 1987; Wallace 2005). In contrast to spider monkeys, however, woolly monkeys will also devote a substantial amount of their time searching for animal prey, which can comprise nearly 10% of their overall diet (Dew 2005; Di Fiore 2004; Di Fiore and Rodman 2001; Stevenson 1992; Stevenson et al. 1994). Spider monkeys and woolly monkeys both live in multimale-multifemale groups with adult sex ratios that are, generally, female biased (reviewed in Di Fiore et al. 2011). The societies of both species are also characterized by fluid association patterns in which subgroup size, membership, and spatial cohesion can change throughout the day (Chapman et al. 1995; Defler 1996; Di Fiore 1997; Hartwell 2016; Link 2011; Nishimura 1990; Peres 1996; Stevenson 2006; Symington 1990; van Roosmalen 1985), although the degree of fission-fusion dynamics is more pronounced in spider monkeys than in woolly monkeys. Males in both taxa are usually philopatric (Di Fiore et al. 2009), with females dispersing from their natal group when they reach sexually maturity, around six years of age (Link et al. 2018; Nishimura 2003; Shimooka et al. 2008; Vick et al. 2008).

Both spider monkeys and woolly monkeys also have relatively "slow" life histories. In wild populations, gestation length is between 7 and 7.5 months, or 229 ± 3 days in spider monkeys and 220 ± 5 days in woolly monkeys (Hartwig 1996). Spider monkeys tend to wean their infants around 24 months after parturition (range 14-31 months; Vick 2008; Di Fiore et al. 2011). The age of weaning for woolly monkeys has not been systematically studied in wild populations, but likely occurs around 18 months of age (range: 10.5-24 months of age, Harvey and Clutton-Brock 1985; personal observation). Interbirth intervals for wild *Ateles belzebuth* and *Lagothrix* spp. have only been calculated from one field site: La Macarena, Colombia. On average, woolly monkeys (*Lagothrix lagotricha*) there give birth every 36.7 ± 4.7 months (Nishimura 2003), while white-bellied spider monkeys at the same site give birth every 43.7 ± 5.1 months (Shimooka et al. 2008).

We tested several predictions derived from the income-capital breeding model to characterize the reproductive patterns of spider monkeys and woolly monkeys at TBS (Table 2.1). If these two atelins are capital breeders, with conception and maintenance of gestation conditional on maternal state, we would expect spider monkeys and woolly monkeys at TBS to exhibit comparable reproductive timing given that they are feeding, primarily, on very similar resources. Specifically, under a capital breeding model, we would predict that matings in both species would increase as fruit becomes more abundant and that conception will occur when maternal body condition is adequate (most likely during or right after the mean peak in fruit availability), with births following 7-7.5 months later. We would also expect to see high variation in interannual birth rates, but low variation in infant mortality. If these two atelins are not capital breeders, however, but rather behave more like relaxed income breeders, then we would expect to see a difference in the timing of reproductive events between the two species. Based on the difference in weaning ages for offspring in the two species, the costliest part of lactation likely differs between woolly monkeys and spider monkeys by several months. Thus, under a relaxed income breeding model, we would predict that spider monkeys should give birth several months earlier than woolly monkeys in a given annual cycle to ensure that mid to late lactation coincides with peak fruit availability. Finally, previous comparisons of phenological patterns between TBS and other field sites inhabited by similar taxa (e.g., Manu, Peru and La

Macarena, Colombia), suggest that fruit availability at TBS is less variable across the annual cycle than other lowland tropical forests (Di Fiore 1997; Link 2011). If so, this leads to the possibility that spider monkeys and woolly monkeys at TBS may be less constrained than other atelin taxa living in more seasonal habitats, and as such, may exhibit less reproductive seasonality with a wider birth window compared to other populations (Di Bitetti and Janson 2000; Janson and Verdolin 2005).

METHODS

Research was conducted at the Tiputini Biodiversity Station (TBS) in the Yasuní Biosphere Reserve of Ecuador. Founded in 1994, TBS encompasses nearly 650 ha of undisturbed primary moist tropical rainforest with an annual rainfall of >2800 mm (Blake et al. 2010; Di Fiore et al. 2009). Although there is not a pronounced dry season, rainfall can vary dramatically between months. March through July are consistently the wettest months of the year with ≥250 mm of rain falling each month. August and September tend to be drier, with rainfall increasing again in October, peaking in November, then drying off again for December and January. Because of its location near the equator, photoperiod is consistent throughout the year, though the timing of sunrise may vary as much as 30 minutes during a biannual cycle. Sunrise occurs earlier in May and November and occurs later in February and August. The field site hosts an intact predator community (Blake et al. 2012) as well as 10 different species of nonhuman primate.

Subjects

Three groups of spider monkeys range at least partially within the 650 ha TBS trail system, and one of these groups (MQ-1) has been monitored regularly since August 2006, with only two periods of observer absence exceeding 2 months (January 2007 through May 2007 and

September 2015 through June 2016). MQ-1 has ranged in size from 23-37 individuals, with an average of 6 adult males and 10 adult females. At least eight social groups of woolly monkeys have been identified to range within the study area. Groups range in size from 14-40 individuals, with typical composition including 2-5 adult males, 4-10 adult females, and 5 or more immatures. Intermittent monitoring of the woolly monkeys began in 2006, with observational data being taken on three groups (D, G, and I) between 2007 and 2009, on two groups (C and G) in 2013, and on four groups (C, D, G, and P) from 2014 to present. For this study, we only considered data collected on woolly monkeys between 2013 and 2016. All spider monkeys and woolly monkeys followed during these study periods were habituated to observer presence, and many of the animals in these groups could be recognized individually based on unique facial markings, pigmentation of the anogenital region, and/or other distinct features such as broken fingers and scars.

Behavioral Data Collection

For both species, behavioral data were recorded using a combination of instantaneous and continuous samples taken during the context of focal follows (Altmann 1974). For spider monkeys, focal animal follows lasting up to 12 hours have been conducted regularly on all adult group members since the onset of study. In 2013, woolly monkey focal follows were twenty minutes long and targeted individuals of all age classes. By 2014, the sampling protocol for woolly monkeys was modified to increase focal follow durations to 2-3 hours. An opportunistic rotating schedule between focal individuals and groups ensured that all adult and subadults were sampled at least once per month. Observations of rare events such as copulations and solicitations between non-focal individuals were recorded *ad libitum*. Copulations were defined as mounting behavior between male and female subjects in which the observer could visibly confirm intromission, or, after dismount, could visually confirm that ejaculate was present. In woolly monkeys, copulations are frequently interrupted by juveniles, and, on occasion, by harassing females (Di Fiore and Fleischer 2005). Therefore, copulations in which a male or female terminated a copulation due to harassment, but then immediately resumed copulating once a harassing individual was chased away or reprimanded, were considered a single event.

Birth and Conception Data

The presence of newborn infants in each of the focal groups of spider and woolly monkeys was recorded opportunistically during group follows. While several infant births could be assigned to an exact day, the majority of infants born during the study were born outside of a specific follow. In these cases, infant birth dates were assigned to the midpoint of the month in which the infant was first seen, unless the infant’s appearance (i.e., fur color and size) suggested to an observer familiar with the development process that they were born in 1-2 months prior. Infant birth dates that could not be estimated to within two months were not included in seasonality analyses; this excluded eight woolly monkey infants born to *Lagothrix* groups D and P between May and October of 2016, a time period in which these two groups were not followed consistently. Birth dates for some spider monkey infants born early in the study were further corroborated through videos and photos collected from 1-2 camera traps monitoring a mineral lick in the group’s home range that was visited frequently (Link et al. 2011; Galvis et al. 2014). The month of conception for each infant was then estimated by subtracting the average gestation length, as reported in Hartwig (1996), from the infant’s assigned birth month.

Fruit Availability

Biweekly estimates of fruit availability at TBS have been collected regularly since September 2006. Following methods set forth in Stevenson (2004), we surveyed nearly 9 km of narrow belt transects that intersect a large portion of the TBS trail system. During each survey we recorded the species (or morphospecies) and diameter at breast height (DBH) of all trees whose crown overlapped the phenological transect and was bearing ripe fleshy fruit (for lianas, the DBH of the main supporting trunk was measured). The basal area, $\pi\left(\frac{\mathrm{DBH}}{2}\right)^2$, was then calculated as a proxy for ripe fruit production (Chapman et al., 1992; Stevenson, 2004) and the effective width of the phenological transects sampled was calculated as the average distance from all identified trees to the center of the transects. The area sampled each monitoring period – calculated as the effective transect width *x* total transect length – was 5.5 ha. For trees and lianas that produced fruits in more than one biweekly period, we assigned a proportion of the tree's basal area following the coefficients of Pascal's triangle, again following Stevenson (2004). For example, if a tree had a basal area of 100 cm^2 and produced fruit during four subsequent monitoring periods, that fruit crop would be distributed among those four periods using Pascal's coefficients of 1:3:3:1, resulting in a basal area score of 12.5 cm^2, 37.5 cm^2, 37.5 cm^2, 12.5 cm^2, for the same respective periods. To estimate habitat-wide fruit availability for a given monitoring period, we summed these portions of the basal area of each tree and liana producing ripe fruits to obtain a total the total basal area of plants bearing ripe fleshy fruits per hectare that period.

We included in analyses of temporal variation in fruit availability only those years of phenological monitoring that were missing data from five or less weekly surveys (N = 7, years: 2008, 2011-2016). For these years, missing biweekly values (N = 10 out of 168 potential values, or 6% of dataset) were imputed using the package MICE (Multivariate Imputation via Chained Equations; van Buuren and Groothuis-Oudshoorn, 2011) in R version 3.1.2 (R Core Development Team, 2014). Five different imputed datasets were created using predictive mean matching, and the average of these datasets were used to represent a final dataset of monthly mean basal area of plants bearing ripe fruit per hectare.

Analyses

We used circular statistics to determine if annual fruit availability and reproductive events for each species could be classified as seasonal. Circular statistics are useful when the distribution of data can be plotted along a circular scale such as compass directions or time (e.g., months, hours in a day, etc.). For our study, we considered the total length of the circular axis to be one year, with each month represented by 30 degrees of that axis. We then converted observations of births, inferred conceptions, and total sum of fruit basal area per month to a vector in which vector length, l, was equal to the cumulative number of events observed that month and the vector angle, a, was equal to the midpoint of that month's 30-degree section (i.e., January = 15 deg, June = 165 deg, and December = 345 deg). The subsequent vectors were then compared to those of a uniform distribution using Rayleigh's test of uniformity (Batschelet 1981). The resulting value is a mean vector length, r, which ranges in values between 0 and 1.0, with 0 indicating an equal distribution of events along the circular axis, and 1.0 indicating an extremely high clustering of events where all events occur during the same interval. Statistical analyses were executed in the circular statistics program for Windows, Oriana v.4 (Kovach 2011).

To better understand the seasonal distribution of observed copulations we calculated the frequency of copulations observed each month as the number of copulations observed divided by the total number of hours that observers followed focal groups that month, and we express the frequency of copulations as the number of copulations per 100 observer-hours. We attempted to remove duplicate observation hours in which multiple observers were following the same subgroup in close proximity. However, this was not always possible for woolly monkeys as groups of this species often range in a dispersed pattern, and observers could be > 100 m from one another viewing different animals yet still be part of the same subgroup. In these cases, we included both observers' hours in the denominator, which means that calculated rates may be under-representative of actual copulation rates in woolly monkeys.

We used Pearson’s ρ correlation to assess the relationship between the average monthly fruit production and the number of observed births, copulations, conceptions, and gestating females per month.

Ethical Note

This research complied with protocols approved by the institutional animal care and use committee (IACUC) at the University of Texas at Austin, adhered to Ecuadorian legal requirements, and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

RESULTS

Woolly monkeys

Between January 2013 and December 2016, we recorded 39 woolly monkey births, 36 of whom were born in to our 4 focal groups, with 3 newborn infants sighted in two neighboring groups during intergroup encounters. All woolly monkey infants with assigned birth months ($N = 31$) were born between May and September, with one exception, a male born in December of 2016 (Fig. 2.1). The monthly distribution of woolly monkey births, collated across years, differed significantly from a uniform distribution (Rayleigh test: $r = 0.636$, $Z = 12.542$, $p < 0.001$). May had the highest number of births followed by another small peak in September, with July as the mean month for woolly monkey births. Although not included in these circular statistical analyses, it should be noted that the 2016 cohorts of *Lagothrix* groups D and P were of similar size and appearance to infants with known birth dates in adjacent groups and, based on observer records, must have been born between April and October of 2016.

While there was little interannual variation in the number of infant births between the years of 2013 and 2015, 2016 was an exception, with twice as many infants born that year in comparison to the previous three years (Table 2.2). Infant sex ratios (male:female) also varied between years and among groups, from 3:1 to 1:1, and were almost always male-biased yielding a cumulative infant sex ratio of 1.57:1. The year 2014 was an exception, when females of *Lagothrix* group D gave birth to 2 females and 0 males. During the four years of the study, only two woolly monkey infants disappeared before reaching two years of age. One infant, born in September 2013, disappeared with his mother between January and March 2015; we do not know if this disappearance represents a dispersal event or a fatality. A second infant, born September 2014, was no longer seen after we found his mother deceased of unknown causes in September of 2015.

We calculated the month of conception for each infant by subtracting the mean gestation length of 220 days from the assigned month of birth. All infants were conceived between October and February, except for one infant born in December 2016, which would have been conceived in May. October was the month with the highest number of conceptions, followed by February, and December was the mean month for conceptions.

Since January 2013, we have observed 170 woolly monkey copulations (Table 2.3). Over 90% of these occurred between August and February, with the frequency of copulations per 100 observation hours peaking in November.

For nine individually recognized woolly monkey females who gave birth between the start of 2013 and end of 2016, the mean number of months between parturition and the first recorded observation of resumed sexual activity was 20.1 months (range: 13-27 months). Mothers of male infants had significantly longer periods of postpartum sexual inactivity (23.3±5.7 mo, N=4) compared to mothers of female infants (17.6±4.5 mo, N = 5; two-sample t= 2.83, df = 7, $p < 0.05$). For five of these females, we could also calculate the length of time between the first observation of resumed sexual activity and successful conception, which averaged 6.4 months, with a range between 2 and 17 months (N = 5).

Spider Monkeys

As for woolly monkeys, the distribution of spider monkey births across the annual cycle also differed significantly from a uniform distribution (Rayleigh test: r = 0.617, Z = 13.308, p <0.001). Since 2006, over 65% of spider monkey births (N = 35) occurred between the months of May and August, and no births were recorded between January and March. Similar to what we found for woolly monkeys, July was the mean birth month for spider monkeys.

On average, three infants were born into the *Ateles* MQ-1 group each year, but as with woolly monkeys, nearly twice as many infants were born in 2016 (N = 7) than was seen in any other previous year (range: 1-4 for years 2006-2015). Yearly infant sex ratios were often female-biased, yielding a cumulative infant sex ratio of 1:1.27 (male:female) over the last twelve years (Table 2.4). Six known infants (3 males, 3 females) have died or disappeared since 2006. All were born between May and August, and a majority of them (N = 4) were only a few weeks old when they vanished. In two cases, both the mother and infant disappeared simultaneously. The death of one male infant in August of 2010 was attributed to suspected infanticide (Alvarez et al., 2015).

Counting back 229 days from the month of birth, we estimated the month of conception for these same 35 infants. Most conceptions (over 65%) occurred between September and December, and, the mean month for conceptions was November.

Due to the formation of consortships in spider monkeys, mating behavior can be notoriously difficult to observe. Thus, despite a much longer period of investigation and a larger number of contact hours compared to the woolly monkeys, we have only seen about a third as many copulations (N=74; Table 2.3). Although copulations were observed year-round, a majority (over 80%) occurred between August and February. As for woolly monkeys, November was the month with the greatest number of copulations seen per 100 observation hours. Again, due to the rarity of observing spider monkey copulations, reported values on mating behavior should be interpreted with caution.

Spider monkey females resumed sexual activity following parturition later than woolly monkey females. Excluding events in which the previous infant died (N = 1) and instances where no copulations were seen prior to conception (N = 1), spider monkey females took, on average, 29.5 months after parturition to being observed to resume mating (range: 17-37 mo, N = 8). Once a female resumed copulating, it then took between 1 and 20 months for her to conceive (average: 7.83 months, N = 6). Of the three females still present in the group after the death or disappearance of their infant, two who lost their offspring during the same month in which they were born were able to conceive 1 and 3 months after parturition, respectively; a third female, whose infant was between 3 and 9 months old when it disappeared, conceived 16 months after parturition.

Fruit Availability

Although the Rayleigh test for fruit availability returned a significant p-value, the low *r* value indicates that the variation in fruit abundance across the year was not demonstrably different from a uniform distribution ($r = 0.163$, $Z = 5.416$, $p < 0.004$). This pattern may be due to an extended period of relatively greater fruit availability, which tends to start increasing in September and usually peaks by March, with a definitive, and abrupt decline occurring immediately after the peak. January was the mean month of peak fruit availability, with the highest estimates of fruit abundance extending from December through March, while May often had the lowest estimates of fruit abundance.

Reproductive events in relation to fruit abundance

In both species, we found a significant negative correlation between average fruit abundance and the number of births in a given month (woolly monkeys: $\rho = -0.860$, $p < 0.001$; spider monkeys: $\rho = -0.836$, $p < 0.001$), with the mean birth month (July) falling in a period when fruit abundance was routinely scarce compared to other months of the year (Fig. 2.2). However, we found no significant relationships between average fruit abundance and either the monthly frequency of observed copulations or conceptions, or the number of gestating females. November, the mean month for conceptions in spider monkeys, and the month with the highest number of observed copulations for both species, falls about two months after fruit availability typically begins increasing and about two months before the mean peak in fruit abundance. Thus, conceptions tend to occur partway through a several month-long period of increasing fruit abundance. A large number of copulations and subsequent conceptions continued to be seen through the end of February, after which time sexual activity and fruit availability rapidly declined. In terms of interannual variation, we found that 2016 – a year in which, for both species, almost twice as many births were seen than in multiple prior years – followed a very strong El Niño event (Climate.gov, 2017) where the period of fruit productivity was prolonged compared to the years that preceded it.

Degree of seasonality compared with Atelins at other field sites

Both woolly monkeys and spider monkeys at TBS showed slightly higher degrees of reproductive seasonality, as measured by r, than did congeners studied at other, more seasonal, field sites (Table 2.5). However, when compared to other genera within the atelin clade, both species in this study had very similar r values to muriquis. Given that r values are susceptible to sample size effects (Janson and Verdolin, 2005), these differences among populations and species should be interpreted with caution.

DISCUSSION

We used long-term demographic, behavioral, and phenological data to compare the timing of reproductive events in two sympatric atelin species in relation to fruit availability. Reproductive events of spider monkeys and woolly monkeys from TBS were distinctly seasonal. Births for both species were concentrated between the months of May and September, a time period in which fruit availability, historically, is at its lowest. In turn, most conceptions occurred between September and January, when fruit availability tends to be increase and is maintained at high-levels throughout the forest. The frequency of observed copulations mapped well onto the conception period, meaning most copulations were observed during times females were most likely to conceive (between August and February, for both species). While some females took just over a year to resume copulating post parturition, others were not observed to copulate for more than two years after giving birth, with the larger-bodied spider monkeys taking ~8 months longer to resume copulating than woolly monkeys. Once females resumed sexual activity, woolly monkeys took on average more than 6 months – and spider monkeys nearly 8 months – to conceive. Despite the fact that the study site is located very near the equator and shows less variation in fruit availability across seasons when compared to other sites, woolly monkeys and spider monkeys at TBS demonstrated slightly greater reproductive seasonality than reported elsewhere.

Reproductive seasonality and the income-capital breeding framework

Collectively, our results suggest that the spider monkeys and woolly monkeys at TBS are better characterized as capital breeders rather than income breeders. First, both species exhibited a clear clustering of births during the same time interval (May-September) and shared the same mean birth month (July). Second, as predicted, the number of copulations observed per month increased as fruit became more abundant. In contrast to our predictions, however, conceptions did not coincide with or follow the mean annual peak in fruit availability. Instead, conceptions occurred before the peak in fruit availability, often by a couple of months. This suggests that females are becoming pregnant partway through a several month long period of generally higher fruit abundance, with the potential to continue accumulating fat stores throughout the early months of gestation. Indeed, woolly monkeys have been noted to undergo substantial seasonal variation in weight gain, often forming large fat deposits throughout the months of greatest fruit availability (Peres 1991, 1993). Moreover, in the Ecuadorian Amazon, indigenous hunters prefer to hunt woolly monkeys between May and August, during the "season of fat monkeys", when the monkeys are found pregnant and at their "fattest" (i.e., more yellow fat is present and the meat is more palatable; Rival 2005: p. 98). Such a seasonal pattern of weight gain has not been reported for spider monkeys, but, given that their diets are comparable to woolly monkeys (e.g., Dew 2005), it is plausible that spider monkeys undergo similar changes in body condition.

The number of births did not vary substantially between years, except, as noted above, in 2016, when both species experienced twice as many births as recorded in several previous years. Interestingly, this spike in births followed an exceptionally strong El Niño event (Climate.gov, 2017), which may have created climatic conditions favorable to fruit production. In 2015, the abundance of ripe fruit increased sooner than seen in previous years and was maintained at a relatively high level for longer, until April of 2016. Such a prolonged period of fruit productivity may have provided a greater opportunity for some females to improve body condition prior to conception, making it more likely for them to conceive and to lay down additional energy reserves during early gestation. Indeed, some of the shortest interbirth intervals in both species were observed following this period. For example, one woolly monkey female that had given birth in June 2014 was able to conceive ~10 months earlier than expected (February 2016), reducing her interbirth interval to 27 months. At least two other woolly monkey females who gave birth in 2014 likely achieved similarly reduced interbirth intervals; however, because these females belonged to *Lagothrix* group D and the birth of their successive infant was not recorded precisely, we can only estimate that the interbirth intervals of these two females were between 24 and 30 months. For spider monkeys, two females who gave birth in 2013 and then again in 2016, had interbirth intervals of 37 and 38 months, respectively, roughly seven months earlier than the average interbirth interval observed at our site (Link et al. 2018). Higher birth rates and shorter interbirth intervals following periods of high fruit availability are not uncommon among primates that follow a capital breeding pattern (e.g., *Macaca fuscicularis* [van Schaik and van Noordwijk 1985, 1999] and *Pongo pygmaeus* [Knott 1998, 2001]), demonstrating that successful female reproduction is inherently tied body condition.

Additionally, following the expectations of a capital breeding pattern, the atelins of TBS experienced little infant mortality. Only two woolly monkey infants disappeared over the four-year period, and over the course of ten years only six spider monkey infants died or disappeared. In spider monkeys, females who lost their infants within the first few weeks and remained in the group were able to conceive between one and three months later, while one female, whose infant disappeared after three months, had to wait an entire year before she could conceive again. Such a pattern may indicate that females who lose infants within the first few months still retain enough energy reserves to successfully conceive and gestate, while females who lose infants after several months may have depleted their energy reserves further than can be replenished either in time to conceive or to successfully carry a pregnancy to term that year, driving them to forego reproduction until the next breeding season.

Low infant mortality rates in capital breeders may be linked to higher rates of prenatal mortality. Because capital breeders rely on energy stores acquired during pregnancy to support lactation later on, females who are unable to procure sufficient energy reserves to continue their current reproductive effort may be forced to abandon their pregnancies in early to mid-gestation (Brockman and van Schaik 2005). In captive primates, capital breeders are known to experience higher rates of fetal loss in early pregnancy than both income-I and income-II (or relaxed income) breeders (Hendrickx and Nelson 1971; Hendrie et al. 1996; Brockman and van Schaik 2005). Although data on prenatal mortality are incredibly difficult to obtain for wild populations, hormonal profiles of female spider monkeys in Panama showed that some females do experience spontaneous abortion (Campbell et al. 2001), and based on the examination of the reproductive organs of wild caught female woolly monkeys (*Lagothrix poeppigii*) in Peru, Bowler and colleagues (2014) were able to estimate that embryo mortality may be as high as 33%.

For capital breeders, the degree of reproductive seasonality is often reduced in captivity (Brockman and van Schaik 2005). Because captive animals are fed a relatively nutritious and consistent diet, their body condition likely remains stable and above the minimum threshold necessary to successfully conceive and gestate, regardless of the time of year. Woolly monkeys and spider monkeys certainly follow this pattern, giving birth throughout the year when held in captivity (Mooney and Lee 1999; Chapman and Chapman 1990), while clearly demonstrating reproductive seasonality in the wild. Given that TBS shows relatively less seasonal variation in fruit production than other tropical sites located farther from the equator, one might expect the degree of reproductive seasonality to be weaker in our atelin populations than at other field sites. However, this was not the case. Contra to expectations, woolly and spider monkeys at TBS were characterized by somewhat higher degrees of seasonality than reported elsewhere for their respective genera. The reason behind such a trend is not clear at this time, although it may be due to limited sample size (Janson and Verdolin 2005). We look forward to seeing if the pattern holds as more long-term data accumulate.

Sex ratios at birth

Sex ratios at birth in primates are often biased towards overproduction of the dispersing sex (Silk and Brown, 2008). In both spider monkeys and woolly monkeys, males appear to be more philopatric than females (Di Fiore et al., 2009), yet only spider monkeys demonstrated long-term birth sex ratios that were female-biased. With only four years of data, however, it is unclear if male-biased sex ratios are the norm for woolly monkeys or just an artifact of our short sampling period. Previous demographic records indicate that between 2008 and 2009, our largest study group (*Lagothrix* group G), had far more immature females than immature males. This is the same study group that had the greatest discrepancy in number of male versus female births over the four-year period described here, suggesting that looking at a longer sampling window could have resulted in a more even birth sex ratio. Indeed, over a 12-year period, the cumulative birth sex ratio of one group of woolly monkeys from La Macarena, Colombia was slightly female-biased at 1:1.2 (Nishimura 2003). In contrast, among closely-related muriquis, birth sex ratios switched from being female-biased to being male-biased (from 67% to 34% female) over a 28-year period, associated with a dramatic increase in group size (Strier and Ives 2012). Similar shifts towards more male-biased birth sex ratios have been observed in red howler monkeys, where they are similarly hypothesized to be linked to increases in population density (Rudran and Fernandez-Duque 2003). While the woolly monkey population at TBS appears to be stable overall, there may be more nuanced competitive or demographic changes within and between groups that influence year-to-year birth sex ratios, and future work should examine how birth sex ratios vary over a longer study period.

Resumption of reproductive activity

After giving birth, spider monkey females took an average of ~8 months longer than woolly monkey females to resume copulating. This should not be surprising given that spider monkey females are both larger than woolly monkey females and exhibit longer periods of infant dependency. During a 23-month investigation of atelin juvenile development at TBS, Schmitt (2009) documented significantly more nursing bouts between spider monkey females and their juvenile offspring than between woolly monkey females and their juvenile offspring, perhaps suggesting a longer period of milk dependency in spider monkeys. If the period of lactation is indeed extended for spider monkeys, then spider monkey females may take longer to recuperate lost energy reserves, and correspondingly, may refrain longer from sexual activity, until their body condition reaches a minimum critical threshold.

Among woolly monkeys, we found a significant difference in the time it took females to resume sexual activity after giving birth based on the sex of her infant. Females who gave birth to a son took nearly 6 months longer to resume copulating than females who gave birth to a daughter. Such a pattern could indicate that male infants place greater energetic demands on their mothers than female infants, or it could represent a mother's differential investment in male versus female offspring. Given that woolly monkeys are sexually dimorphic (males are larger than females), differences in male and female growth trajectories may lead to unequal energetic demands on the mother, whether through lactation effort and milk production or the cost of transporting a heavier infant. Longer durations and greater energetic costs of postnatal maternal care for sons compared to daughters has been observed in a number of primates, including spider monkeys (Symington 1987; Chapman and Chapman 1990), chimpanzees (Nishida et al. 2003), mountain gorillas (Eckardt et al. 2016), and Hanuman langurs (Ostner et al. 2005).

Future directions

Due to the "slow" life histories of atelin primates, important reproductive parameters, such as age of first reproduction and interbirth intervals, can be extremely difficult to estimate in the absence of long-term data. We view this paper as a first step towards providing some of these important data and towards understanding the reproductive patterns of the atelin primates at TBS. Given that female body condition likely plays an important role in atelin reproduction, we believe a productive area for future research will involve regular, non-invasive tracking of female body condition, reproductive function, and fecundity using physiological markers (e.g., fecal progesterone to monitor a female's reproductive state and urinary c-peptide to monitor body condition [reviewed in Behringer and Deschner 2017]), particularly in relation to fruit availability. It will also be informative to investigate further the influence of infant sex on maternal investment and energetic expenditure.

TABLES

Table 2.1. Patterns and predictions regarding the timing of reproductive events in relation to food availability under different models.

	Model		
Reproductive Stage	Income-I Breeder	Income-II Breeder	Capital Breeder
Conception	-Cued exogenously -Narrow conception window	-Cued exogenously and endogenously -Flexible conception window	-Cued endogenously -Variable conception window
Gestation	-Little to no fat accumulation during pregnancy -Low prenatal mortality rates		-Accumulate fat reserves throughout pregnancy -High prenatal mortality rates
Birth	-Little interannual variation in birth rates -Births occur during the mean peak in food abundance	-Births occur before the mean peak in food abundance	-High interannual variation in birth rates -Births occur after the mean peak in food abundance by a period of time equal to the delay in conception plus the gestation length
Lactation		-Mid to late lactation coincides with mean peak in food abundance	
Weaning	-High variation in infant mortality rates -Weaning occurs during mean peak in food abundance		
Infant Survival	-High variation in infant mortality rates -Survival will be higher for infants born during the mean peak in food abundance		-Low variation in infant mortality rates

Table 2.2. Number of male and female woolly monkeys born each year to four different study groups (Lagothrix groups C, D, G, and P) and their cumulative infant sex ratios (ISR).

	Group C		Group D		Group G		Group P		Group Totals		
Year	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	ISR (M:F)
2013	1	1	1		2			1	4	2	2:1
2014				2	3	1	1	1	4	4	1:1
2015	1	1	1				2	1	4	2	2:1
2016	2		2	1	3	3	3	2	10	6	1.67:1
Total	4	2	4	3	8	4	6	5	22	14	1.57:1

Table 2.3. Total number of observation hours and the total number of observed copulations for each month, summed across years in spider monkeys (N=10 years) and woolly monkeys (N=4 years).

	Observed Copulations *Ateles*			Observed Copulations *Lagothrix*		
Month	Contact Hours	No.	No./100 hrs	Contact Hours	No.	No./100 hrs
January	1475.5	4	0.271	1413.7	8	0.566
February	1795.6	11	0.613	1264.3	19	1.503
March	1285.5	4	0.311	812.3	3	0.369
April	1380.5	2	0.145	1142.9	0	0.000
May	1637.8	3	0.183	916.0	4	0.437
June	1462.7	1	0.068	1490.4	2	0.134
July	1735.9	2	0.115	2421.6	6	0.248
August	1598.6	10	0.626	1659.0	13	0.784
September	1308.6	7	0.535	805.5	25	3.104
October	1384.2	8	0.578	1237.0	24	1.940
November	1259.6	18	1.429	1045.6	50	4.782
December	774.6	4	0.516	1037.6	16	1.542
Total	17099.1	74	0.433	15246.0	0	1.115

Table 2.4. Number of male and female spider monkeys born each year in one group of Spider monkeys (Ateles MQ-1) and the cumulative infant sex ratio (ISR).

Year	No. of Males	No. of Females	No. of Unknown	Cumulative ISR (M:F)
2006	1	2		1:2
2007	1	2		1:2
2008	1			1:1.25
2009	2	3		1:1.4
2010	1	2		1:1.5
2011		3		1:2
2012	3	1		1:1.44
2013		2		1:1.67
2014	2			1:1.36
2015		1	1	1:1.45
2016	4	3		1:1.27

Table 2.5. Seasonality in fruit availability and births as measured by Raleigh’s r among several atelin primates.

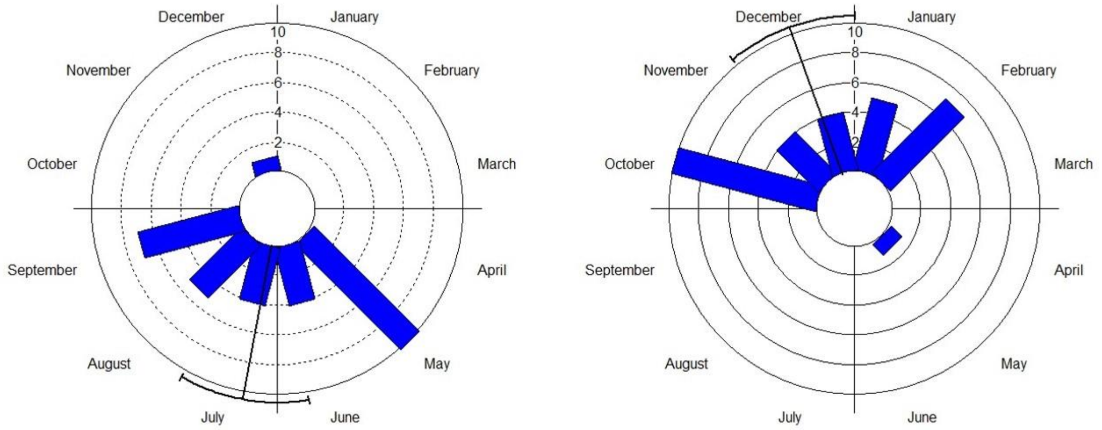
Species	Site	Latitude	*r* fruit	*r* births	n	*P*	References
Ateles belzebuth	La Macarena, Colombia	2°40' N	0.489	0.491	6	NS	Klein 1971
Ateles belzebuth	TBS, Ecuador	0°40' S	0.163	0.617	35	<0.001	This study
Ateles geoffroyi	BCI, Panamá	9°9' N	0.225	0.539	18	<0.005	Milton 1981
Ateles paniscus	Manu, Perú	11°55' S	0.283	0.370	46	<0.005	Symington 1987
Brachyteles arachnoides	Caratinga, Brazil	19°50' S	0.211	0.629	57	<0.001	Strier 1996b; Strier et al. 2001
Lagothrix lagotricha lugens	La Macarena, Colombia	2°40' N	0.489	0.589	20	<0.001	Nishimura et al. 1992
Lagothrix lagotricha poeppigii	TBS, Ecuador	0°40' S	0.163	0.636	31	<0.001	This study

FIGURES

Figure 2.1. Circular plot showing the distribution and mean of a) woolly monkey births and b) conceptions from 2013-2016 (N = 31) and of c) spider monkey births and d) conceptions from 2006-2012 (N = 35) at the Tiputini Biodiversity Station in Ecuador. The timing of births/ conceptions across months is significantly different from a uniform distribution in both woolly monkeys (Z = 13.308, p<0.001) and spider monkeys (Z = 12.542, p <0.001). The mean month for births is July for both species, and the mean month for conceptions is December for woolly monkeys and November for spider monkeys.

A) *Lagothrix* births

B) *Lagothrix* Conceptions



C) *Ateles* births

D) *Ateles* conceptions

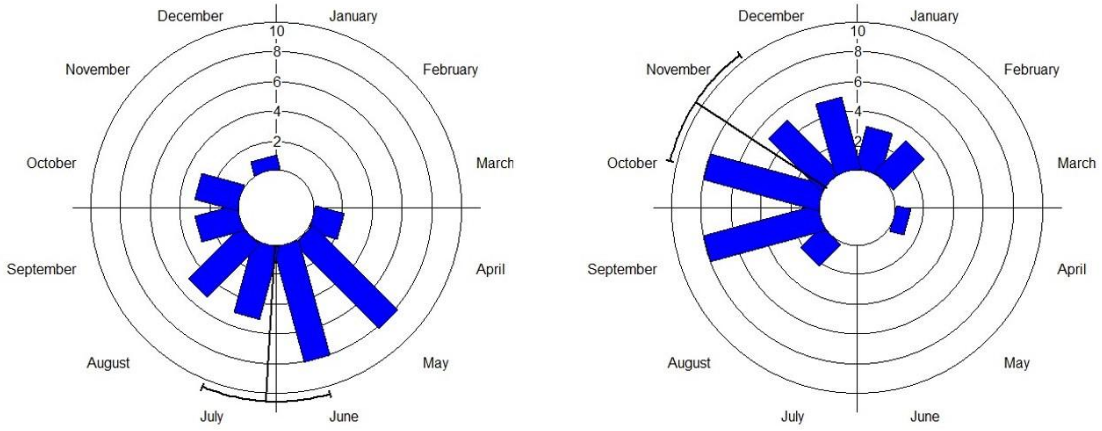
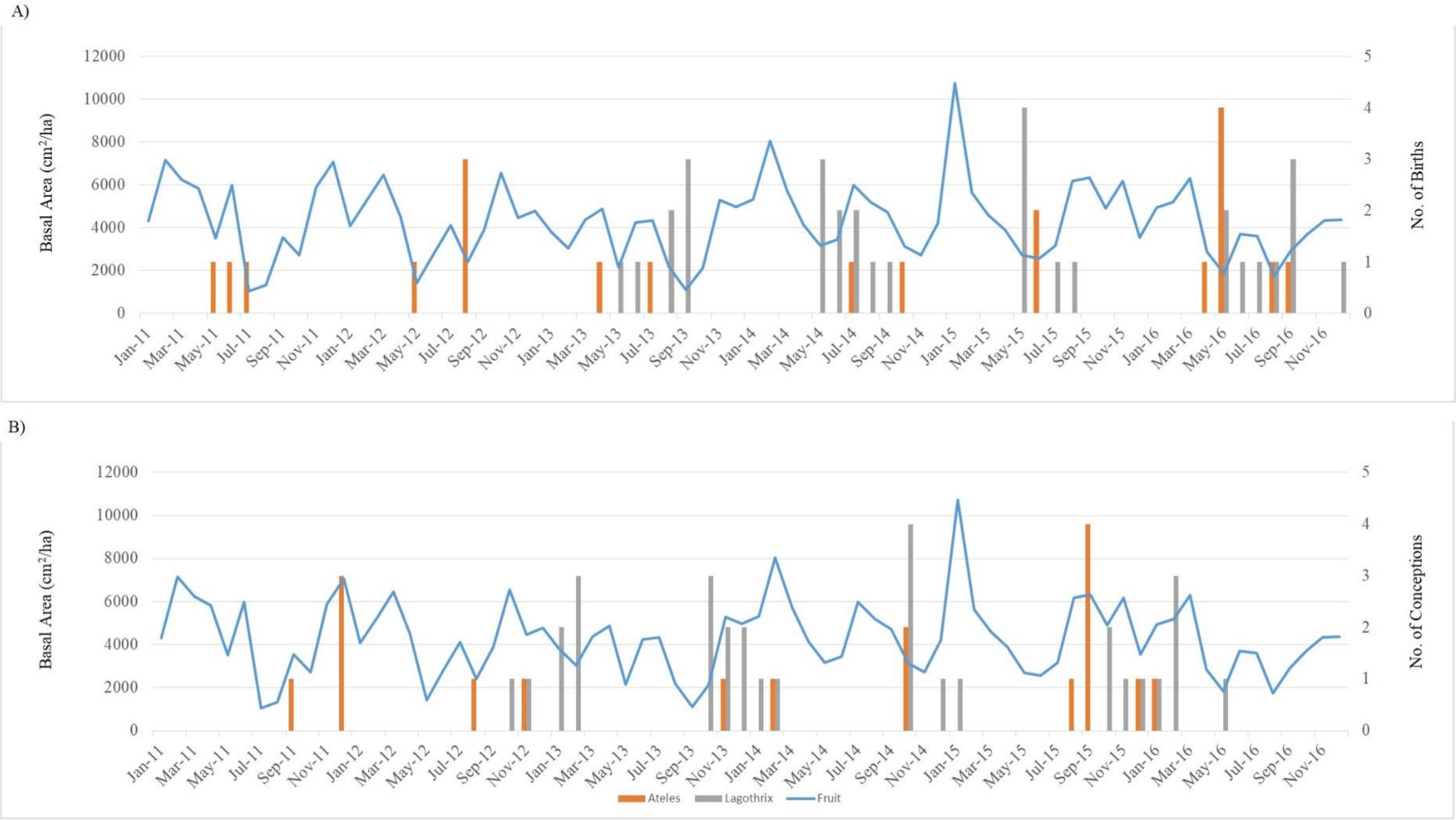


Figure 2.2. The number of woolly and spider monkeys a) births and b) conceptions between January 2011 and December 2016 in relation to monthly estimates of fruit abundance (measured as the proportion of the basal area (cm2/ha) of plants bearing ripe fruits) at the Tiputini Biodiversity Station, Ecuador. Births were negatively correlated with monthly averages of fruit abundance (woolly monkeys: ρ = -0.860, p < 0.001; spider monkeys: ρ = -0.836, p < 0.001), but no relationship was found between fruit availability and the number of conceptions.



Chapter 3: Variation in space use and social cohesion within and between four groups of woolly monkeys (*Lagothrix lagotricha poeppigii*) in relation to fruit availability and mating opportunities at the Tiputini Biodiversity Station, Ecuador

INTRODUCTION

For group-living organisms, daily activities such as traveling, foraging, and resting are rarely performed in isolation, and individuals' movement patterns are often dependent on one another. As such, there is a growing understanding among animal ecologists that many movement processes must be considered and quantified within a social context (Westley et al. 2018). By studying the concurrent movements of more than one animal, researchers are better able to elucidate how competitive dynamics both within and between social groups – including attraction to or avoidance of particular individuals or sets of individuals – may influence overall patterns of space use and access to critical resources, such as sleeping sites, food, and mates (Kays et al. 2015).

Animal ecologists and behavioral biologists have also increasingly come to appreciate the high degree of variation and complexity that exists in the spatiotemporal association patterns of group-living animals (e.g., Aureli et al. 2008; Whitehead 2008). In many species, individuals live, travel, and forage together in cohesive units typically referred to as "social groups", where these groups can be identified as the set of animals that regularly are seen in spatial proximity to one another and who interact, at least much of the time, in a tolerant or affiliative manner. In some species, however, socio-spatial associations are more transient and flexible, with individuals associating and interacting at different points in time with varying sets of other animals. Species that exhibit these higher degrees of “fission-fusion” social dynamics may form subgroups with stable and predictable membership, such as the single male units in multilevel societies of geladas or hamadryas baboons (Grueter et al. 2012), or they may form subgroups with more individualistic and flexible subgroup membership, as commonly observed in spider monkeys, chimpanzees, dolphins, or hyenas (reviewed in Aureli et al. 2008).

Members of the ateline clade of primates (howler monkeys, spider monkeys, woolly monkeys, and muriquis) show a range of association patterns with varying degrees of flexibility in size, composition, and spatial cohesion of groups over time, ranging from one single cohesive group (e.g., some species of howler monkeys) to groups showing high degrees of fission-fusion dynamics where individuals or subgroups remain separated from one another for several hours or even days (e.g., spider monkeys; Di Fiore et al. 2011). Such dynamic grouping patterns are thought to reflect an optimization strategy by which individuals actively balance the costs and benefits of group living (Chapman and Chapman 2000; Lehmann and Boesch 2004; Aureli et al. 2008). Costs most often include competition over preferred, ephemeral food items, such as ripe fruits, that occur in discrete patches too small to support all group members simultaneously (Klein and Klein 1977; Wrangham 1980, 1986; Symington 1990), while benefits may include the ability to adaptively respond to perceived risks of predation (Andres Link et al. 2011) or shifting reproductive opportunities (Goodall 1986; Symington 1987a; Chapman 1990; Hashimoto et al. 2001; Anderson et al. 2002; Mitani et al. 2002; Shimooka 2003). Because larger groups must commonly travel farther per day to compensate for faster depletion rates than smaller groups, subgrouping behavior and adjustments to subgroup size may further reflect strategies to reduce relative ranging costs (Asensio et al. 2009; Chapman et al. 1995; Chapman and Chapman 2000; Janson and Goldsmith 1995).

In this chapter, we present a detailed description of ranging patterns and subgrouping behavior among four neighboring groups of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) living in a tropical rainforest in eastern Ecuador. Similar to other large-bodied atelines, woolly monkeys live in large mixed-sexed groups with adult sex ratios that are generally female biased (reviewed in Di Fiore et al. 2011). Males are usually philopatric (Di Fiore et al. 2009) with females dispersing from their natal groups when they reach sexually maturity, at around six years of age (Akisato Nishimura 2003). Woolly monkeys are highly frugivorous, preferring ripe fruit and supplementing their diet with young leaves, shoots, and flowers (Defler and Defler 1996; Dew 2005; Di Fiore 2004; Peres 1994; Stevenson 1992; Stevenson et al. 1994). However, unlike other atelines – and despite their large body size – woolly monkeys also devote a substantial amount of time searching for and consuming animal prey (Dew 2005; Di Fiore 2004; Di Fiore and Rodman 2001; Stevenson 1992; Stevenson et al. 1994). Similar to spider monkeys and muriquis, woolly monkeys are further characterized as having long periods of infant dependency, and they demonstrate reproductive seasonality in which most mating behavior and reproductive milestones (e.g., conceptions and births) are clustered to a few months out of the year (Nishimura, 2003; Ellis et al. in review).

Early reports on patterns of spatial cohesion and grouping dynamics among woolly monkeys were equivocal, and descriptions have ranged from social groups that appear to exhibit high degrees of fission-fusion dynamics (Kavanagh and Dresdale 1975) to social groups that remained relatively cohesive throughout the day, albeit highly spread out (Nishimura 1990, 1994; Peres 1996; Di Fiore 1997). Such varied assessments most likely stemmed from the high spatial dispersion of woolly monkey social groups as they perform their daily activities, with group members often spread over several hundred meters (Di Fiore 1997; Peres, 1996), thus limiting the ability of a single observer to visually detect more than a subset of individual group members at any given time.

Although precise quantitative metrics of grouping dynamics and social cohesion are still lacking (Aureli et al. 2008; Stevenson 2006), woolly monkeys are, at present, most commonly characterized as living in relatively cohesive social groups that occasionally fission into tightly-grouped feeding parties and/or coordinated subgroups that persist for hours or even days (Defler 1996; Di Fiore 1997). Subgroup composition is generally mixed-sex (Peres 1996), but solitary males and all-male subgroups have also been observed (Di Fiore et al. 2009). Cohesion and coordination among the members of social groups and subgroups is often mediated through the frequent use and reciprocation of low-volume contact calls. In some studies, measures of group cohesion (e.g., group spread and inter-individual distance among groupmates) have been shown to be negatively correlated with both fruit availability (Peres, 1996) and group size (Zárate and Stevenson 2014), meaning that groups spread out more in times of low fruit availability and that members of larger groups are separated by greater distances, on average, than members of smaller groups, presumably in response to within-group feeding competition. However, to our knowledge, no study has investigated how temporal variation in available mating partners also may affect subgrouping behavior and group cohesion, despite its influence on subgroup size and composition in a number of other primate taxa, including chimpanzees (Goodall 1986; Matsumoto-Oda et al. 1998; Boesch and Boesch-Achermann 2000; Wrangham 2000; Hashimoto et al. 2001; Anderson et al. 2002; Mitani et al. 2002) and spider monkeys (Symington 1987; Chapman 1990; Shimooka 2003).

Adding more complexity, woolly monkeys do not actively defend exclusive areas of their home range (i.e., they are non-territorial [Burt 1949]), and the home ranges of neighboring groups can overlap extensively (45-100%) (Di Fiore 2003; Di Fiore et al. 2011). In these shared areas, groups occasionally encounter one another, with varying degrees of acceptance or tolerance shown towards members of other groups. Thus, at times, socially cohesive groups will coalesce with others to form temporary “supergroups” that rest, travel, and forage together for up to several hours (Defler 1996; Di Fiore 1997; Di Fiore et al. 2009; A. Nishimura 1990; Peres 1994). Likewise, subsets of individuals from different neighboring social groups have also been observed to form subgroups that range independently from the rest of the members in each of their respective social groups (Ellis et al. 2014). Individuals have also been noted to occasionally visit other social groups for varying periods of time without conflict (Nishimura 1990, 2003). However, in contrast to these tolerant associations, some intergroup encounters among these same groups are clearly hostile and are accompanied by distressed vocalizations, display behavior (e.g., branch shaking, conspicuous branch crashing), and chasing or lunging at members of the opposing group (Di Fiore, 1997). The factors determining why some intergroup encounters in woolly monkeys are peaceful, while others are hostile, remain to be investigated, but may be related to location of encounters, the identity and composition of the groups involved, the specific interaction history of those groups, or the presence of particular individuals, as well as to seasonal variation in food resources and mating opportunities (e.g., Fashing 2001; Crofoot et al. 2008; Koch et al. 2016).

While a number of studies have described ranging behavior and space use patterns of woolly monkeys, particularly in relation to fruit availability (reviewed in Di Fiore et al. 2011), few have focused on multiple social groups at the same site or have considered how variation in spatial cohesion and subgrouping dynamics, both within and between Lagothrix groups, may affect observed ranging patterns (but see Peres, 1996), nor have they considered how the availability of both food and mating opportunities might concurrently impact ranging and subgrouping behavior. Here we use a combination of location and subgroup composition records collected over 14 months by multiple observers following animals from four neighboring social groups of *Lagothrix lagotricha poeppigii* [1] to describe subgrouping behavior and ranging patterns and [2] to examine variation in spatial cohesion among animals within and between groups, over time and in relation to both food availability and mating opportunities. Our study is unique in that observers worked in tandem and could individually recognize animals from multiple social groups and thus were able to collect precise data on subgroup compositions (including on subgroups comprising animals from different social groups) and on inter-individual and inter-subgroup distances. Individual identifications were corroborated, post hoc, with genotype data collected for the same animals over time to ensure consistency in identity assignment across time.

We first summarize subgrouping behavior and within social group cohesion for each of the four study groups, including the percent of time that social groups divide into subgroups, variation in subgroup size, and spatial dispersion between focal individuals within and between subgroups. We then present data on ranging and space use for each of the four social groups, including information on daily path length, home range size, core area size, and patterns of range overlap. Rates of intergroup encounters are then compared to indices of overlap among the home ranges of the different social groups to determine if intergroup encounters occur more or less often than expected by chance. Finally, we evaluate how these patterns of group cohesion, subgroup size, and ranging behavior vary with temporal fluctuations in both habitat wide estimates of ripe fruit availability and the availability of mating opportunities.

METHODS

DATA COLLECTION

Study Site

This study was conducted at the Tiputini Biodiversity Station (TBS) in lowland Ecuador. The research station is located along the northern bank of the Tiputini River (76°08’W, 0°38’S) and is part of the Yasuní Biosphere Reserve, one of the largest remaining tracts of western Amazonian lowland rainforest. Laid out over a series of rolling hills and drainages, an extensive network of well-marked trails provides access to nearly 650 ha of terra firme and seasonally flooded forest. Annual rainfall at the field site generally exceeds 2800 mm (Blake et al. 2010; Di Fiore et al. 2009), with March through July often marked as the wettest months of the year. Fruit abundance varies throughout the year, with January through March typically showing the greatest abundance of ripe fruit and July and August the smallest abundance of ripe fruit (Snodderly et al. in review). The field site hosts an intact predator community (Blake et al. 2012) and 10 different species of nonhuman primate, including three atelines: lowland woolly monkeys (*Lagothrix lagotricha poeppigii*), red howler monkeys (*Alouatta seniculus*), and white-bellied spider monkeys (*Ateles belzebuth*).

Study Population

At least eight socially cohesive woolly monkey groups have been identified to range, entirely or partially, within the TBS trail system. These social groups vary in size from 13-40 individuals, with typical composition including 2-5 adult males, 4-10 adult females, and 5 or more immatures. At some point in time between 2006 and the present, at least one individual from each of these eight social groups (referred to as Lagothrix A, C, D, G, HP, I, L, and P) was anesthetized via remote intramuscular injection of either ketamine HCl or a reconstituted mixture of tiletamine HCl and zolazepam HCl (Zoletil®) using a CO2-powered darting rifle. While anesthetized, animals were fitted with a TelonicsTM or HolohilTM VHF transmitting radiocollar to facilitate tracking via radiotelemetry. Social groups with radiocollared animals were then the subjects of at least occasional contact during successive field seasons for the lifetime of the collar on the animal (i.e., until either the radiocollar battery expired, the animal lost the collar or disappeared from the group, or the animal died and the collar was recovered). The radiocollars were useful for confirming and monitoring the presence of, at minimum, the collared individual in a particular social group, even without visual contact with that individual. Over the years and across different researchers, woolly monkey groups at the site have been studied at varying intensities, with more consistent behavioral and ranging data being collected on groups D, G, and I between 2008 and 2009, on groups C and G in 2013, and on groups C, D, G, and P from 2014 to the present.

Behavioral Data

The present study focuses on the behavioral and spatial data collected by KME and seven field assistants between August 2014 and December 2015, excluding January 2015 to March 2015, on four of the known social groups at the site: Lagothrix C, D, G, and P. These groups occupied contiguous home ranges within the TBS trail system and were previously well habituated to observer presence. Animals were individually recognized by the presence of radiocollars with identification tags, facial scarring, variation in pelage color, broken digits, and/or differences in anogenital size and pigmentation. Following Schmitt and Di Fiore (2014), we estimated each individual's age-sex category based on external morphology and behavior. The number of adults and subadults in these four study groups varied between 8 and 19 individuals, with total group size, including juveniles and infants, ranging from 14 to 30 individuals (Table 3.1).

Behavioral data were recorded using a combination of instantaneous and continuous sampling in the context of day-long focal follows (Altmann 1974). Due to the dispersed nature of woolly monkey social groups, a strict schedule of rotating among predetermined focal animals was not feasible. Instead, observers were assigned a particular social group, and once members of that social group were located, observers opportunistically selected one adult or subadult to follow as their focal subject. When selecting a focal animal, preference was given to individuals with the fewest number of accumulated hours of focal sampling for that given month. In cases where social groups were fissioned into two or more subgroups and when there were fewer eligible focal animals within a subgroup than observers, supernumerary observers were tasked with searching throughout the assigned social group's home range for eligible animals in other subgroups to follow. During focal animal follows, the behavior of the focal individual and the identity and distance category (contact, <1 m, <5 m, <10 m) of each neighbor within a 10 m radius were recorded instantaneously every 5 minutes. Feeding behavior and social interactions were recorded continuously. Rare events such as mating behaviors (e.g., copulations, mating solicitations) between non-focal individuals were recorded ad libitum.

Every 15 minutes (on the hour and at 15, 30, and 45 minutes after the hour), observers evaluated subgroup composition and recorded the identity and/or age-sex class of each subgroup member, the general activity of the majority of subgroup members ('Resting', 'Moving', ‘Foraging’, ‘Socializing’), and an estimate of subgroup spread (i.e., distance between the farthest two subgroup members, in meters). We defined a subgroup as a subset of individuals that maintained visual or low intensity vocal contact with one another 15 minutes before, during, or after the sampling (Bezanson et al. 2008; Chapman et al. 1995) and were located at a distance of < 100 m from at least one other subgroup member following a chain rule (e.g., Ramos-Fernández 2005). Social groups were thus considered “subgrouped” when the number of individuals present during consecutive sampling periods were fewer than the total group size and those individuals remained out of visual and vocal contact with other members of their social group for two or more sampling points. Subgroup determinations were often corroborated through telemetry checks in which observers scanned the vicinity for radiocollared animals belonging to the social group being followed.

Simultaneous observers continuously monitored the location (using a datalogging GPS: see below), dimension, and cohesion of subgroups being followed, regularly alerting one another to their focal individual’s position within the subgroup, as well as the arrival and departure of other individuals, through a series of ‘whoop' vocalizations and two-way walkie-talkie radios. Typically, there would be one to three observers in the field simultaneously monitoring different individuals from the same social group, but on rare occasions, up to five observers collected focal data simultaneously on different members of the same social group. Focal animal behavioral data and subgroup composition data collected concurrently from different subjects allowed us to measure the spatial dispersion between pairs of individuals within a subgroup as well as the spatial dispersion between individuals in two or more subgroups. To reduce spatial and temporal autocorrelation in ranging analyses, we pooled together all simultaneously recorded subgroup composition and location records in which multiple observers were following focal animals within the same subgroup. For these cases, subgroup location was assigned as the average location between all observers tracking that subgroup. We followed different social groups from dawn to dusk (circa 06:00 – 18:00) on a rotating schedule, contacting each group on average 4-8 times per month (range: 3-19 days), contingent upon weather and the number of eligible focal individuals in each group.

To aid in the collection of ranging data, each observer was assigned a handheld GPS unit (Garmin 76CSx or GPSMap64) that was programmed to store the observer's location every ~20 seconds, and observers attempted to always remain underneath members of the subgroup being followed and within 10 horizontal meters of their focal subjects. Subgroup locations were subsequently determined by extracting locations from the observer's 'tracks' at the same 15-minute sampling points where subgroup composition was recorded. Location records were collected in the WGS84 coordinate system and projected to Universal Transverse Mercator (UTM 18S) units. To compensate for the minor positional errors inherent in GPS readings, we averaged the locations of all fixes recorded in the 2-minute window surrounding the time of interest when extracting a location from the GPS track. For example, to extract a location for 09:00, we would average the set of ~6 locations recorded between 08:59 and 09:01. When possible, subgroup locations were additionally recorded in geometric vector notation from a previously georeferenced landmarks (i.e., the distance and angle from a marked and mapped tree or trail marker).

In some cases, it was impossible to collect or extract a location for a particular sampling point, either [1] because of observer or GPS error (e.g., failure to record a location), [2] because the observer was not positioned close enough to the subgroup (e.g., because the monkeys crossed over a flooded area that was inaccessible to terrestrial observers), or [3] because of poor GPS coverage. In these cases, if possible, we reconstructed a location for the sampling point based on linear extrapolation from the surrounding records. We reconstructed up to a maximum of two successive location points in this manner.

Intergroup Encounters

Intergroup encounters (IGEs) were recorded opportunistically any time an individual from another social group was visually or acoustically observed to be within 100 m of an observer's focal subgroup. During IGEs, observers recorded the identities and/or age-sex class of as many members from the other social group as possible, as well as the location of the encounter and the general activity of both groups prior to, during, and after the IGE. The IGE was considered to have ended when individuals from each social group were once again separated by >100 m.

Fruit Availability

Biweekly estimates of fruit availability at TBS have been collected regularly since September 2006. Following methods outlined in Stevenson (2004), we surveyed nearly 9 km of narrow belt transects that intersect a large portion of the TBS trail system. During each survey we recorded the species (or morphospecies) and diameter at breast height (DBH) of all trees whose crowns overlapped the phenological transect and were bearing ripe, fleshy fruit (for lianas, the DBH of the main supporting trunk was measured). The basal area of the trunk ,$\pi\left(\frac{\mathrm{DBH}}{2}\right)^2$, was then calculated as a proxy for ripe fruit production (Chapman et al. 1992;

Stevenson 2004), and the effective width of the phenological transects sampled was calculated as the average perpendicular distance from all monitored trees to the center of the transects. The total area sampled each monitoring period, calculated as the effective transect width x total transect length, was 5.25 ha. For trees and lianas that produced fruits in more than one biweekly period, we assigned a proportion of the tree's basal area to each fruiting period following the coefficients of Pascal's triangle, again following Stevenson (2004). For example, if a tree had a basal area of 100 cm2 and produced fruit during four successive monitoring periods, the basal area index of ripe fruit production would be distributed among those four periods using Pascal's coefficients of 1:3:3:1, resulting in proxy scores of 12.5 cm2, 37.5 cm2, 37.5 cm2, 12.5 cm2, for the same respective periods. To then index habitat-wide fruit availability for a given monitoring period, we summed these portions of the basal area of each tree and liana producing ripe fruits and divided by the total area sampled to obtain the total basal area of plants bearing ripe, fleshy fruits per hectare that period.

Mating Opportunities

Because we were not monitoring female reproductive hormone profiles, precise measures of female estrous cycles and receptivity are not available for the time period in question. Therefore, to characterize the availability of potentially receptive females (i.e., mating opportunities) across the landscape during this study, we used a behavioral indicator: the total number of different individual females who were observed copulating across all four study groups in a given month. To correct for differences in behavioral sampling intensity across months, we divided this value by the number of cumulative observer hours for that same month to yield a mating opportunity index, which we present as the number of different females seen copulating per 100 observation hours. Mating behavior in woolly monkeys is a fairly conspicuous activity, with solicitations and copulations occurring in front of other group members. Furthermore, the frequency of observed mating behavior and rates of conception have been found to be highly correlated (Chapter 2 and Ellis et al. in review).

ANALYSES

Home Range Size and Overlap

A total of 11,853 15-minute subgroup location records were collected during subgroup follows, with an average of 2,963 ± 646.7 location records collected per social group (Table 3.2). From these records, we computed annual and monthly kernel density estimates of habitat utilization for each social group. Home ranges constructed from kernel density estimates (KDE) are based on use distributions and correspond to the minimum area for which the probability of locating a given social group is equal to the probability specified. Following Laver and Kelly's (2008) recommendation, we used the 95% KDE isopleth to define each social group’s home range, as it is one of the most commonly used contour values and allows for more consistent comparisons across studies. Each social groups’ “core area” was defined as the 50% KDE isopleth.

A key parameter in constructing biologically meaningful home ranges is the bandwidth, or smoothing parameter (h). Small values of h tend to undersmooth data, creating fragmented home range contours, whereas large values of h tend to oversmooth the data, leading to an overestimation of home range size and incorporating excessive space around the outermost locations (Kie et al. 2010). We chose to use an ad hoc (had hoc) smoothing parameter as this method has provided better results compared to using the reference (href) or least-squared cross-validation (hlscv) smoothing factors, which tend to oversmooth and undersmooth the data, respectively (Kie 2013). Starting with an initial smoothing parameter of h = 50 m and iteratively adding 5 m up to h = 100 m, we found that an ad hoc smoothing parameter of h = 85 m was sufficient for yielding a contiguous 95% KDE isopleth for each study group without adding excessive space around the outermost locations. Prior to constructing home range contours, we employed an incremental area analysis (Kenward and Hodder 1996) to ensure that home range areas reached an asymptote and were thus a good estimate of home range size. Home range contours were constructed in R version 3.3 (R Core Team 2016) using the ‘adehabitatHR’ package (Calenge 2006) and imported into ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA) for visualization.

We assessed the monthly variation in shared space use between social groups using two measures of overlap. The first measure investigates how far a neighboring group penetrates into a focal group’s home range and is taken as the ratio between the area of overlap between the two groups and the total area of the focal group’s home range, resulting in two values per dyad. However, this measure does not account for the time each group spent in the area of overlap (e.g., two groups may have high degrees of overlap, but spend relatively little time in those overlap zones). Therefore, as a second measure of shared space use we calculated the utilization distribution overlap index (UDOI). This index is similar to Hurlbert's (1978) index of niche overlap and has been suggested to be the most appropriate index when trying to quantify overlap in terms of common space use within a particular period of time (Fieberg and Kochanny 2005).

Values of this index generally range between 0 and 1, with 0 indicating that two home ranges do not overlap at all and 1 indicating that home ranges are uniformly distributed and overlap perfectly. In some cases, if the utilization distributions being compared are not uniformly distributed and there is a high degree of overlap, UDOI may be >1.

Daily Path Length

We calculated daily path lengths (DPL) as the Euclidean distance displacement of successive ranging locations recorded during subgroup follows. We performed such calculations for all follows lasting 10.5 hours or more (N = 114), as there was no significant difference between follows lasting 10.5 – 11.75 hours (N = 88) compared to follows lasting 12 – 12.25 hours (N = 26) (t = -0.256, df = 112, p-value = 0.798). Because members of a given social group may fission from and coalesce into different subgroups throughout the day, some individuals from the same social group may travel farther than others. To account for this variation, we calculated DPLs for all unique focal individuals followed on a given day when they were in different subgroups and averaged the length of these unique paths to provide a single DPL estimate for the social group that day.

Factors Influencing Subgrouping, Group Cohesion, Ranging Patterns, and Intergroup Encounters

To investigate the effects of social group size, fruit availability, and mating opportunities on observed patterns of subgrouping, group cohesion, and ranging, we used a combination of mixed effects models. First, we evaluated the probability of a social group being divided into one or more subgroups using a generalized linear mixed effects model (GLMM) for proportions fit with a binomial error distribution and logit-link. The response variable was the proportion of subgroup composition records (SGC) records collected for which a social group was observed "subgrouped" in relation to total number of records collected for that group during the month, with social group size, the monthly estimate of fruit availability, and the mating opportunity index set as fixed effects. Variation in average monthly subgroup size and interindividual distance were evaluated with linear mixed effects models (LMM), again with group size, the monthly estimate of fruit availability, and the mating opportunity index set as fixed effects. Variation in DPL was also examined using LMM, and fixed effects included the social group's average subgroup size on the day the length of the daily path was collected, as well as the monthly estimate of fruit availability, and the mating opportunity index. Variation in home range size, core area size, and their corresponding overlap were also evaluated with LMMs. In these models, group size, the monthly estimate of fruit availability, and the mating opportunity index were set as fixed effects. In all models, group sizes and subgroup sizes only included adult and subadult individuals, as the movement decisions of juveniles and infants are largely dependent on those of their mothers.

Prior to inclusion in models, all predictor variables were converted into unitless Z scores to remove the undue influence of using variables measured in different units (e.g., group size measured as an integer number versus fruit basal area measured as cm2/ha). In LMMs, all response variables associated with size or distance (e.g., subgroup size, interindividual distance, DPL, home range size, and core area size) were log transformed, while estimates of overlap were square-root transformed using $\sqrt{Y + 0.5}$. Given that our data included repeated measures on the same social group and uneven sampling of groups across months, we included social group ID and the combination of month and year data were collected as random effects. All models were fit with the lmer and glmer functions found in the R package ‘lme4’ (Bates et al. 2015), and corresponding p values were calculated using lmerTest (Kuznetsova et al. 2014).

To select the combination of predictor variables best fitting each dataset, we used the Aikaike’s Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). The model with the lowest AICc score was considered the best fitting model. However, in cases where the next best-fitting model was within two AICc points, indicating a plausible alternative, we preferentially selected the model that was most parsimonious (i.e., the model with the fewest fixed effects) (Burnham and Anderson, 2002). We also calculated the relative importance of each fixed effect from the sum of AICc weights across candidate models. All AICc associated metrics were performed in R using the dredge function of the ‘MuMin’ package (Barton, 2016). Finally, we report the significance of the final model compared to the null model using log-likelihood ratio tests calculated with the anova function in R.

RESULTS

Group Cohesion

Of the location records collected between August 2014 and December 2015, 10,859 had accompanying subgroup composition (SGC) records, and of these records, 10,743 included one or more individuals from our four focal study groups (Lagothrix C, D, G, and P). Overall, social groups C and D were subgrouped in 62% and 59% of SGC records, respectively, while groups G and P were subgrouped in 85% and 83% of SGC records, respectively. Monthly variation in the proportion of 15-min SGC samples in which social groups were "subgrouped" was best predicted by social group size and the mating opportunity index, but not fruit availability (Table 3.3, Table 3.4), with larger groups tending to be subgrouped more often and all groups subgrouping less often when more mating females were present in the population. For each standard deviation increase in social group size, the chances of being found "subgrouped" increased 3.5-fold, and for each standard deviation increase in the mating opportunity index, the chances of being "subgrouped" decreased by a factor of 0.42.

Excluding subgroup composition records collected during IGEs (n = 829 of 10,743 records), subgroup sizes ranged from 1-17 individuals (Fig. 3.1). Despite a two-fold difference in total social group size, the median subgroup size across the four study groups was similar, ranging between 7 and 8 individuals. Contrary to our expectations, our measure of monthly habitat-wide ripe fruit availability was not a significant predictor of average subgroup size. We also found that total social group size was not a significant predictor of average subgroup size, suggesting that social groups, regardless of size, nonetheless break into similarly sized subgroups. Instead, monthly variation in subgroup size was best predicted by the mating opportunity index, with subgroup size increasing as the number of different females seen copulating across all four study groups increased (Table 3.3, Table 3.4). In all social groups, subgroups were predominantly mixed-sex (88.6%), although 8.2% and 3.2% of subgroup composition records consisted of single- or all-female subgroups and single- or all-male subgroups, respectively.

Interindividual distances between members of the same social group were estimated from 5,150 15-min SGC samples where two observers were simultaneous with more than one member of the same social group and collected location records. The average distance between individuals from the same social group who were associating in the same subgroup (N = 4,011 of these simultaneous location records) was ~42 m and ranged between 0 and 493 m, while distances between individuals from the same social group who were simultaneously followed while in different subgroups (N = 1,139) ranged from 112 to 1,252 m (Fig. 3.2). As expected, social group size had a significant and positive effect on the average distance between simultaneously followed group members each month (Table 3.3, Table 3.4). This is not surprising, as larger groups were more often divided into subgroups than were smaller groups, and the subgroups into which larger groups were split frequently traveled farther apart from one another (N = 906, average: 412±244 m) than the subgroups of smaller groups (N = 233, average: 244±112 m). However, contrary to our expectations, fruit availability had no effect on the average distance between simultaneously followed group members each month, nor did the mating opportunity index.

Daily Path Length

Combining daily path length data for the four focal study groups, the average distance traveled each day was 1,887 m (N = 114, range: 922 – 3,695 m; Table 3.5). Although group size varied substantially across groups, daily path lengths were not significantly different between groups (Kruskal-Wallis test: H = 5.405 df = 3, p = 0.14). Eight of the 114 daily path lengths calculated were missing complementary subgroup composition records and subsequently excluded from the LMM exploring the effects of subgroup size, fruit availability, and mating opportunities on daily path length. After accounting for repeated measures and uneven sampling across groups over time, neither subgroup size, nor fruit availability, had a significant effect on daily path length (Table 3.4). However, a group's daily path length was significantly and positively related to the mating opportunity index, with DPLs increasing by 15% for every standard deviation increase in the number of copulating females observed that month (Table 3.6).

Home Range Size and Overlap

Home ranges for each social group across the entire study period – defined as the 95% isopleth of kernel density estimates – ranged from 93 ha (group C) to 204 ha (group D) (Table 3.7, Fig. 3.3). Overall, groups C, G, and P used, on average, 60-70% of their home range when followed each month, whereas group D only used, ~45% of their home range when followed each month. Core areas for the entire study period, defined as the 50% isopleth of kernel density estimates, ranged in size from 25 ha (group C) to 53 ha (group D). On average, the monthly core areas of groups C and G represented ~20% percent of their overall home range, while the core areas of groups D and P only represented 12% and 16% of their respective home ranges. Group size had a significant effect on monthly home range size, with larger groups having larger home ranges (Table 3.6, Table 3.4). However, the significance of this effect is just below the 0.05 probability threshold and should be taken with caution. Neither monthly fruit availability nor our index of mating opportunities were significant predictors of monthly home range size. Similarly, when evaluating monthly variation in core area size, we found no effect of group size, fruit availability, or the mating opportunity index, with AICc values and likelihood ratio tests indicating that none of the alternative models fit significantly better than the null model (Table 3.4).

Home range and core area overlap, taken as the percent of home range or core area a focal group shares with a neighboring group, varied extensively over time and between pairs of groups (Table 3.8). Home ranges calculated for the entire study showed that focal groups shared between 2.7% (C and P) and 67.8% (C and G) of their home range with a neighboring focal group, with an average of 22.6±20.8%. Core areas calculated for the entire study period revealed that only groups C and G had overlapping portions of their core areas at this time scale, with group C sharing 28.4% of its total core area with group G, and group G sharing 19.8% of its total core area with group C. At a monthly time scale, multiple pairs of groups were found to share portions of their core areas with one another. On average, groups shared 4.8±6.4% of their monthly core area with a neighboring focal group, but this value was highly variable across months (range: 0% and 50%). Despite monthly variation in average percent home range and core area overlap between groups, we found no relationship between these measures and either fruit availability or mating opportunities (Table 3.4). It should be noted, however, that these overlap values only include the four focal groups, and considerable overlap may exist between the focal groups and neighboring groups not included in this study (e.g., the home ranges of at least two other social groups are known to overlap that of group D to the east and northwest of its home range).

Shared space use on a monthly scale, as measured by UDOI, also varied between pairs of groups and across months. Groups C and G exhibited the highest monthly UDOI values (average: 0.235±0.145), spending more time in their shared home range than other pairs. Considering only months in which the 95% KDE contours overlapped, the UDOI values for other pairs of groups were relatively low in comparison (average: 0.084±0.124), indicating that despite home range overlap, these other pairs used less of their overlap area in the same month than groups C and G. As observed for monthly estimates of home range and core area overlap, neither fruit availability nor mating opportunities had an effect on the time groups spent in shared areas (Table 3.4).

Intergroup Encounters

Over the entire study period, we recorded 102 IGEs, 61 of which occurred directly between two or more of our focal study groups, and 41 of which occurred between a focal group and a neighboring but non-focal social group. Nearly 60% of these IGEs were considered "tolerant" associations, where affiliative behaviors (e.g., grooming bouts and copulations) were sometimes observed between members of different groups, as well as more neutral interactions in which members from different groups could be seen traveling or feeding less than 10 m from one another with no accompanying agonistic behavior. Distressed vocalizations (e.g., "clucking", which is characteristic of agitation or uneasiness), display behaviors (such as branch shaking), and/or chasing and lunging at members of opposing groups occurred in 33% of IGEs. Avoidance behavior (i.e., a group's leaving an area immediately following the detection of non-group members prior to confrontation) was seen in 6% of IGEs, although this number is likely to be underestimated as observers may often have failed to detect the presence of members from another social group during non-agonistic IGEs. Excluding time spent in overnight associations, IGEs lasted an average of 122 mins and ranged from between several minutes to entire days. The locations of intergroup encounters were not limited to the periphery of a group's home range. In fact, 88 of the 102 IGEs had one or more location records sampled during the span of the IGE that fell within the monthly core area of at least one of the interacting groups.

A strong majority (73.8%) of the IGEs recorded between focal study groups, occurred between groups C and G. Overall, these two groups had a rate of 0.30 encounters per 12 hours of observation time with either group, or slightly less than one IGE every three days. In comparison, the pair of groups with the next highest encounter rate (groups D and G) had only 0.05 encounters per 12 hours, or roughly one IGE every 20 days. As expected, the observed rate of intergroup encounters among pairs of groups each month was highly and significantly correlated to their monthly UDOIs ($R^2 = 0.762$, df = 45, $p < 0.001$).

Finally, on 18 occasions we observed subgroups that were formed by a subset of individuals belonging to separate social groups. Individuals from groups C and G formed a majority (72.2%) of these mixed-group subgroups, followed by members of groups D and G (11.1%). Mixed-group subgroups almost always included both males and females, the exception being 45 minutes in which a female and her juvenile from group C traveled with several females and their dependents from group G before being joined by an adult male, also from group G. Mixed-group subgroups would often travel, feed, socialize, and rest as a cohesive unit. These associations lasted from 60 minutes up to full days, and in some cases persisted overnight (N = 5). The average subgroup size for mixed-group subgroups was 8 individuals (range: 4-12), similar to that of subgroups comprising members of only one social group. We should note that we do not include in this overview of mixed-group subgroups the occasional visits that some unknown, extragroup individuals – males and females alike – would make to our focal social groups. Although visiting animals could stay in association with group members for several hours up to several days, we did not know what social group they were from, nor if they were in the act of potentially immigrating or emigrating.

DISCUSSION

Together, our results demonstrate that lowland woolly monkeys at the Tiputini Biodiversity Station, show both flexible and fluid association patterns, with subgroup size, composition, and cohesion changing throughout the day and across months. These results also reinforce earlier speculation about the dynamic and variable nature of woolly monkey association patterns (Di Fiore 1997; Di Fiore and Strier 2004; Kavanagh and Dresdale 1975; Peres 1996). However, these dynamic grouping patterns vary considerably from those observed in classically described "fission-fusion" societies. Unlike the individualistic form of fission-fusion dynamics exhibited by spider monkeys and chimpanzees, or the predictable subgrouping patterns observed in geladas or hamadryas baboons, woolly monkeys appear intermediary between these two extremes (Aureli et al. 2008; Di Fiore and Strier 2004; Kummer 1968, 1971). While social groups could be found ranging as a cohesive unit (i.e., where all group-members were observed within 100 m from at least one other group member), finding them separated into two or more subgroups was much more common, particularly among the larger groups.

In species showing a high degree of fission-fusion dynamics, changes in subgroup size and cohesion are often thought to reflect an adaptive response to within group feeding competition over patchily distributed resources (e.g., ripe fruit), and, as such, larger more cohesive subgroups are expected during periods of higher food availability (Wrangham 1977, 1980, 1986; Symington 1990; Chapman et al. 1995; Boesch 1996; Chapman and Chapman 2000; Newton-Fisher et al. 2000; Anderson et al. 2002; Mitani et al. 2002; Shimooka 2003; Asensio et al. 2009). In the present study, however, we found no relationship between habitat wide estimates of fruit availability and measures of either subgrouping (i.e., the monthly proportion of subgroup composition records in which groups were divided into subgroups and average subgroup size) or intragroup cohesion (i.e., interindividual distance of simultaneously followed group members) among the four social groups. This result may not be that surprising given that previous studies on the grouping dynamics and feeding ecology of spider monkeys and woolly monkeys within Yasuní found the same lack of relationship between estimates of fruit availability and measures of within group feeding competition (Di Fiore 2003, 2004; Di Fiore and Rodman 2001; Link 2011). For example, for woolly monkeys at a nearby field site (the Proyecto Primates Research Area, located about 35 km from the TBS site), the proportion of the monthly diet comprising ripe fruit (a preferred resource) was not correlated with habitat wide ripe fruit availability, nor were feeding party sizes particularly well predicted by feeding patch size (as measured by diameter at breast height; Di Fiore 2004). Moreover, habitat wide estimates of ripe fruit availability accounted for only 23% of the observed variation in subgroup size among sympatric white-bellied spider monkeys (*Ateles belzebuth belzebuth*) at TBS (Link, 2011). Such weak relationships may stem from the relatively persistent availability of fruit resources and the less markedly seasonal variation in fruit production at Yasuní compared to other Amazonian sites, but the dispersed spatial organization of woolly monkeys while engaged in subsistence activities and their devotion to searching for animal prey likely also play important roles (Di Fiore, 2004; Di Fiore and Rodman, 2001).

Subgrouping behavior may also reduce the relative ranging costs individuals incur at larger group and subgroup sizes due to scramble competition (Asensio et al. 2009; Chapman et al. 1995; Chapman and Chapman 2000; Janson and Goldsmith 1995). However, despite variation in both overall group sizes and subgrouping behavior among the four groups, we found no relationship between daily path length and total group size, nor did we find that larger subgroups had longer average daily paths. Again, this lack of relationship may be due to the greater spatial dispersion and less synchronized behavior of individual woolly monkeys as they perform their daily activities, leading to a relaxation of scramble competition among groupmates. Indeed, it was rare to see all subgroup members occupy feeding trees simultaneously. Instead, typically only a small subset of subgroup members would enter a single feeding tree at a time, while the remaining members either rested, foraged on food items found in other tree crowns and lianas, or searched for arthropods and other animals (Di Fiore 2004; Peres 1996). Stemming from this observation is the consideration that subgrouping and resultant ranging patterns may not be reflective of intragroup feeding competition, but rather of an inability to coordinate activities at larger group and subgroup sizes (Dias and Strier 2003). This consideration may help explain why we see larger groups splitting into subgroups more often than smaller groups, yet find no differences in daily path lengths. Speculatively, the fact that all four social groups exhibited median subgroup sizes of 7-8 individuals may indicate that there is an upper threshold to the number of animals that can successfully coordinate their activities at any given time.

Interestingly, while subgrouping and ranging behavior were not demonstrably related to fruit availability, both fission-fusion dynamics and daily path length were strongly predicted by our behavioral index of mating opportunities. We found that as the number of observed sexually active females increased across the landscape, social groups were more likely to stay cohesive (i.e., less likely to fission) and to be seen in larger, mixed-sex subgroups. This result is consistent with observations of a number of other primates that are also characterized by high fission-fusion dynamics and polygynandrous mating systems (e.g., chimpanzees [Goodall 1986; Boesch 1996; Matsumoto-Oda et al. 1998; Wrangham 2000; Hashimoto et al. 2001; Mitani et al. 2002] and spider monkeys [Symington 1987; Chapman 1990; Shimooka 2003]), although mating opportunities are seldom formally discussed as a potential driver of fission-fusion dynamics in these taxa. Taken together with the fact that woolly monkeys demonstrate strong reproductive seasonality, where mating behavior and major reproductive events (i.e., conceptions and births) are each limited to several months out of the year (Nishimura, 2003; Ellis et al. in review), the subgrouping dynamics of woolly monkeys at TBS may best be explained by variation in reproductive opportunities, rather than foraging costs and intragroup feeding competition.

The ranging patterns (DPLs and home range sizes) of the four social groups at TBS were, overall, very similar to those reported for two social groups followed by Di Fiore (2003) at the nearby Proyecto Primates Research Area in Yasuní, with daily path lengths from both sites typically falling between 1,700 and 2,100 m, and annual home ranges between 93 ha and 204 ha. Although we found a significant and positive relationship between group size and home range size at the monthly scale, the largest overall home range was occupied by group D, one of our smallest groups. The large home range of group D is enigmatic, but may be a reflection of poorer habitat quality or the uneven distribution of key resources within their home range (Ganas and Robbins 2005; Isbell et al. 1998), especially given that location records for that group were generally concentrated in the periphery and relatively sparse near the center of their KDE-defined home range (Fig. 3.3). Subjectively, the “center” of group D’s home range was not habitually used for resting or foraging, but rather was simply traversed on the way to more productive areas. Another potential reason why the long-term home range of group D was larger than that of other groups may be that they were undergoing a home range shift throughout the course of the study, as evidenced by increased and more repeated use of the northwest portion of their home range as the study progressed. In chimpanzees and gorillas, such shifts have been observed after the disappearance of neighboring groups (Nakamura et al. 2013), as the direct result of mating competition (Watts 1998), and from the splitting and formation of new groups

(Caillaud et al. 2014; Watts 1998). What may have prompted a home range shift in group D is not entirely clear, but may include the loss of several adult males between 2014 and 2015 and the potential immigration of new adult males from a neighboring group, HP, whose home range overlapped with that of group D to the northwest. Molecular analyses from non-invasively sampled individuals in both social groups are currently underway to shed light on this possibility.

Long-term home range overlap among neighboring woolly monkey groups at TBS was extensive and comparable to that reported at other sites (reviewed in Di Fiore et al. 2011, but see Shanee 2014), although at finer time scales (i.e., monthly values) the extent of home range overlap between neighboring groups was often reduced. Core area overlap, on the other hand, was always rare, with only groups C and G sharing significant portions of their long-term core areas, although some pairs of groups did share core areas at the monthly time scale. Given that most pairs of neighboring groups had minimal core area overlap – and given that the percent of overlap experienced by groups was often reduced at finer time scales – there may be support for the idea that woolly monkeys retain exclusive access to at least some portions of their home ranges (predominantly their core areas) over short temporal scales. This may be surprising given that woolly monkeys are considered non-territorial and do not actively defend their home range from conspecifics. Still, recent evidence has shown that mountain gorillas – also considered non-territorial – may nonetheless maintain exclusive access to a majority of their core areas through active avoidance of neighbors (Seiler et al. 2017). Similarly, non-territorial baboon troops with substantial degrees of home range overlap demonstrate an avoidance-based spacing pattern, with less spatial overlap and less time spent in areas of overlap at finer time scales (Markham et al. 2013). Given that measures of concurrent space use by neighboring groups of woolly monkeys (UDOI), approached 0 for almost all pairs of groups examined (groups C and G were an exception), temporal partitioning of space is potentially one such mechanism by which woolly monkey groups may reduce direct competition with their neighbors.

Rates of intergroup encounters were highly correlated with monthly measures of shared space use. As such, they varied substantially between neighboring groups, with groups C and G meeting each other on average once every three days, while other neighboring pairs of groups only encountered each other once every twenty days, on average. During intergroup encounters, interactions observed between members of different groups ranged from affiliative (e.g., copulation) and tolerant (e.g., co-feeding in food trees) to moderately hostile (e.g., display behavior, chasing), with more than half of IGEs classified as the former. The duration of intergroup encounters varied from as little as several minutes to several hours and even overnight associations, indicating that although woolly monkeys may attempt to avoid their neighbors in some contexts, they may also seek out and maintain associations with members from other social groups in others. This impression is highlighted by the occasional formation of mixed-group subgroups, that also lasted from several hours to overnight. Individuals may opt to maintain spatial proximity to extragroup members in order to minimize the risk of predation, glean information about the availability or location of food resources, gain access to reproductive opportunities, or investigate groups into which they may transfer to in the future (e.g., macaques [Majolo et al. 2005; Zhao 1997]). Furthermore, tolerant intergroup encounters may be facilitated by high levels of genetic relatedness between individuals residing in neighboring groups, as has been suggested for western gorillas (Bermejo et al. 2004; Bradley et al. 2004). Given the genetic evidence that both male and female woolly monkeys potentially disperse from their natal groups (Di Fiore et al. 2009) and the identification of at least one mother-son dyad residing in separate, but neighboring social groups (Ellis and Di Fiore, unpublished data), we find this an attractive explanation and will be investigating its plausibility in further work.

The movement ecology paradigm, at its core, attempts to understand how and why animals move the way they do (Nathan et al., 2008). For group-living animals, such as woolly monkeys, the movements of any given individual are often influenced by social cues from and interactions with both habitual groupmates and extragroup individuals, some of whom may be familiar and perhaps even related animals. As such, attempts to analyze movement of individuals without considering social interactions and group dynamics may be misleading (Langrock et al. 2014). In this chapter, we explicitly explored broad scale patterns of ranging and space use among four groups of woolly monkeys living in lowland Amazonia as they related to fission-fusion dynamics and temporal variation in fruit availability and mating opportunities. The woolly monkeys of the Tiputini Biodiversity Station exhibited highly flexible and fluid association patterns, both within and between social groups. Contrary to our expectations, these dynamic grouping patterns were not related to intragroup feeding competition, but rather reflected variation in potential mating opportunities across time. For animals inhabiting rich environments – where food resources may be relatively predictable in time and space – the location and number of potential mates should also be included in models predicting movement and grouping patterns. The ability of woolly monkeys to maintain social cohesion and coordinate movements at larger group and subgroup sizes may also be a constraint on association patterns, resulting in larger groups dividing into subgroups more often than smaller groups.

The ability of group-living animals to coordinate their ranging behavior has long fascinated researchers, and recent advances in both technology and computational methods have encouraged the integration of collective behavior research with that of the movement ecology paradigm (Westley et al. 2018), providing promising new insights into how animals use social cues to make decisions about travel. Although woolly monkey social groups may use avoidance-based spacing mechanisms to reduce direct competition with neighboring groups, some individuals may also seek out affiliative interactions with conspecifics from other groups, as evidenced by the occurrence of tolerant intergroup encounters and affinitive interactions we recorded among the members of mixed-group subgroups. Together, our data on woolly monkey ranging behavior highlight the necessity to include social dynamics and social context into models of animal movements and emergent patterns of space use.

TABLES

Table 3.1 Composition of four woolly monkey groups between August 2014 and December 2015 at the Tiputini Biodiversity Station, Ecuador.

	Group C		Group D		Group G		Group P	
Age-Sex	2014	2015	2014	2015	2014	2015	2014	2015
Adult Male	2	3	5	4	3	4	4	4
Subadult Male	1	-	1	-	2	2	-	1-2
Adult Female	5	4-5	6	5-6	10-11	8-9	9	10
Subadult Female	1	1	-	-	4	3-4	2	2
Juvenile	5	4	5	5	6	7	7	7
Infant	-	1-2	2	1	4	2	2	3
Adults and Subadults	9	8-9	12	9-10	19-20	17-19	15	17-18
Total with Dependents	14	13-15	19	15-16	29-30	26-28	24	27-28

Table 3.2. Number of independent location records used to construct each group's monthly 95% and 50% KDEs. In parentheses is the number of days each group was contacted per month.

Group	Aug-14	Sep-14	Oct-14	Nov-14	Dec-14	Apr-15	May-15	Jun-15	Jul-15	Aug-15	Sep-15	Oct-15	Nov-15	Dec-15	Grand Total
C	278 (6)	252 (7)	207 (5)	276 (7)	35 (2)	157 (6)	189 (6)	176 (6)	818 (19)	325 (10)	143 (3)	116 (4)	137 (6)	202 (5)	3311
D	107 (3)	242 (6)	239 (7)	195 (6)	21 (1)	111 (5)	120 (3)	152 (7)	240 (6)	234 (7)	125 (3)	187 (5)	126 (3)	224 (7)	2323
G	434 (7)	360 (8)	273 (8)	122 (5)	32 (2)	173 (9)	338 (9)	338 (8)	507 (12)	451 (10)	220 (6)	159 (6)	45 (5)	241 (10)	3693
P	182 (5)	154 (3)	268 (7)	143 (3)	45 (2)	117 (5)	202 (3)	183 (4)	271 (5)	316 (6)	224 (5)	162 (6)	81 (4)	178 (6)	2526
Grand Total	**1001**	**1008**	**987**	**736**	**133**	**558**	**849**	**849**	**1836**	**1326**	**712**	**624**	**389**	**845**	**11853**

*More location records were acquired in July and August of 2015 due to an increased number of personnel

Table 3.3. Results of the final generalized linear mixed model and linear mixed models predicting the effects of group size, fruit abundance, and mating opportunity index on observed patterns of subgrouping and within group cohesion. In all models, group ID and month-year were set as random effects.

Test	Response Variable	Fixed Effects	Estimate	Std. error	z or t value	*p*-value
Probability of Subgrouping GLMM with proportions family: binomial link: logit)	# SGC records where social group is "subgrouped"/ # Total SGC records	(Intercept)	1.161	0.347	3.343	<0.001
		Social Group Size	1.262	0.166	7.614	<0.001
		Mating Opportunity Index	-0.842	0.266	-3.169	<0.002
		Model Fit: $\chi2= 101.73$; $p<0.001$				
Subgroup Size LMM	Average Monthly SG size	(Intercept)	2.009	0.055	36.541	<0.001
		Mating Opportunity Index	0.140	0.024	5.914	<0.001
		Model Fit: $\chi2= 16.664$; $p<0.001$				
Interindividual Distance LMM	Average Monthly Interindividual Distance (m)	(Intercept)	4.25	0.1909	22.264	<0.001
		Social Group Size	0.3623	0.1228	2.952	0.041
		Model Fit: $\chi2= 7.392$; $p<0.007$				

Table 3.4. Candidate models and subsequent selection (in bold) examining the influence of group size (GS), subgroup size (SGS), fruit availability (FA) and mating opportunity index (MO) on estimates of subgrouping behavior, within group cohesion, ranging patterns, and range overlap. Random effects include Group ID (ID) and the combination of Month and Year (MY) data were collected. Models are ranked from lowest AICc to highest. Relative importance of each predictor variable based on sum of AIC weights.

<table>
<tr><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th colspan="4">Relative Importance</th></tr>
<tr><th></th><th>Test</th><th>Response Variable</th><th>Models</th><th>df</th><th>AICc</th><th>ΔAICc</th><th>w_i</th><th></th><th>GS</th><th>SGS</th><th>FA</th><th>MO</th></tr>
<tr><td>Subgrouping and Cohesion</td><td>**Probability of Subgrouping**
GLMM with proportions family: binomial link: logit)</td><td># SGC records where social group is "subgrouped" / total # of SGC records</td><td>**GS + MO + (1|ID) + (1|MY)**</td><td>**5**</td><td>**1552.40**</td><td>**0.00**</td><td>**0.71**</td><td></td><td>1.00</td><td>NA</td><td>0.23</td><td>0.92</td></tr>
<tr><td></td><td></td><td></td><td>GS + FA + MO + (1|ID) + (1|MY)</td><td>6</td><td>155.84</td><td>2.45</td><td>0.21</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>MO + (1|ID) + (1|MY)</td><td>4</td><td>1557.37</td><td>4.97</td><td>0.06</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>FA + MO + (1|ID) + (1|MY)</td><td>5</td><td>1559.77</td><td>7.38</td><td>0.02</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + (1|ID) + (1|MY)</td><td>4</td><td>1645.10</td><td>92.71</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + FA + (1|ID) + (1|MY)</td><td>5</td><td>1647.46</td><td>95.07</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>1 + (1|ID) + (1|MY) [NULL]</td><td>3</td><td>1649.32</td><td>96.92</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td>**Subgroup Size**
LMM</td><td>Average SG size</td><td>**MO + (1|ID) + (1|MY)**</td><td>**5**</td><td>**-25.01**</td><td>**0.00**</td><td>**0.61**</td><td></td><td>0.21</td><td>NA</td><td>0.21</td><td>1.00</td></tr>
<tr><td></td><td></td><td></td><td>GS + MO + (1|ID) + (1|MY)</td><td>6</td><td>-22.45</td><td>2.57</td><td>0.17</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>FA + MO + (1|ID) + (1|MY)</td><td>6</td><td>-22.44</td><td>2.57</td><td>0.17</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + FA + MO + (1|ID) + (1|MY)</td><td>7</td><td>-19.75</td><td>5.26</td><td>0.04</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>1 + (1|ID) + (1|MY) [NULL]</td><td>4</td><td>-10.81</td><td>14.20</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>FA + (1|ID) + (1|MY)</td><td>5</td><td>-8.74</td><td>16.27</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + (1|ID) + (1|MY)</td><td>5</td><td>-8.51</td><td>16.51</td><td>0.00</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td>**Interindividual Distance**
LMM</td><td>Monthly Average Interindividual Distance (m)</td><td>**GS + (1|ID) + (1|MY)**</td><td>**5**</td><td>**86.44**</td><td>**0.00**</td><td>**0.51**</td><td></td><td>0.92</td><td>NA</td><td>0.20</td><td>0.29</td></tr>
<tr><td></td><td></td><td></td><td>GS + MO + (1|ID) + (1|MY)</td><td>6</td><td>88.15</td><td>1.71</td><td>0.22</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + FA + (1|ID) + (1|MY)</td><td>6</td><td>89.08</td><td>2.64</td><td>0.14</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>GS + FA + MO + (1|ID) + (1|MY)</td><td>7</td><td>91.04</td><td>4.60</td><td>0.05</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>1 + (1|ID) + (1|MY) [NULL]</td><td>4</td><td>91.25</td><td>4.81</td><td>0.05</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>MO + (1|ID) + (1|MY)</td><td>5</td><td>93.09</td><td>6.65</td><td>0.02</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>FA + (1|ID) + (1|MY)</td><td>5</td><td>93.80</td><td>7.36</td><td>0.01</td><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Table 3.4 continued.

Ranging and Overlap	**Daily Path Length** LMM	Daily Path Length (m)	FA + MO + (1|ID) + (1|MY)	6	-12.10	0.00	0.38	NA	0.33	0.57	0.97
			MO + (1|ID) + (1|MY)	**5**	**-11.47**	**0.63**	**0.28**				
			SGS + FA + MO + (1|ID) + (1|MY)	7	-10.70	1.40	0.19				
			SGS + MO + (1|ID) + (1|MY)	6	-9.95	2.15	0.13				
			1 + (1|ID) + (1|MY) [NULL]	4	-5.43	6.68	0.01				
			SGS + (1|ID) + (1|MY)	5	-4.29	7.81	0.01				
			FA + (1|ID) + (1|MY)	5	-3.43	8.67	0.00				
	Home Range Size LMM	Monthly HR Size (Ha)	GS + (1|ID) + (1|MY)	5	-10.80	0.00	0.55	0.92	NA	0.24	0.21
			GS + FA + (1|ID) + (1|MY)	6	1.16	2.25	0.18				
			GS + MO + (1|ID) + (1|MY)	6	1.49	2.58	0.15				
			1 + (1|ID) + (1|MY) [NULL]	4	3.83	4.91	0.05				
			GS + FA + MO + (1|ID) + (1|MY)	7	3.85	4.93	0.05				
			FA + (1|ID) + (1|MY)	5	6.10	7.18	0.02				
			MO + (1|ID) + (1|MY)	5	6.26	7.34	0.01				
	Core Area Size LMM	Monthly CA Size (Ha)	**GS + (1|ID) + (1|MY)**	**5**	**8.93**	**0.00**	**0.50**	0.90	NA	0.28	0.21
			GS + FA + (1|ID) + (1|MY)	6	10.75	1.82	0.20				
			GS + MO + (1|ID) + (1|MY)	6	11.48	2.55	0.14				
			1 + (1|ID) + (1|MY) [NULL]	4	13.23	4.30	0.06				
			GS + FA + MO + (1|ID) + (1|MY)	7	13.33	4.40	0.06				
			FA + (1|ID) + (1|MY)	5	15.10	6.17	0.02				
			MO + (1|ID) + (1|MY)	5	15.61	6.68	0.02				
	Home Range Overlap LMM	Monthly HR Overlap (%)	**1 + (1|ID) + (1|MY) [NULL]**	**4**	**591.37**	**0.00**	**0.53**	NA	NA	0.28	0.27
			FA + (1|ID) + (1|MY)	5	593.28	1.91	0.20				
			MO + (1|ID) + (1|MY)	5	593.34	1.97	0.20				
			FA + MO + (1|ID) + (1|MY)	6	595.33	3.96	0.07				
	Core Area Overlap LMM	Monthly CA Overlap (%)	**1 + (1|ID) + (1|MY) [NULL]**	4	**494.81**	**0.00**	**0.50**	NA	NA	0.26	0.32
			MO + (1|ID) + (1|MY)	5	496.29	1.48	0.24				
			FA + (1|ID) + (1|MY)	5	196.94	2.13	0.17				
			FA + MO + (1|ID) + (1|MY)	6	498.45	3.64	0.08				
	Utilization Distribution Overlap Index LMM	Monthly UDOI of 95% KDE Contours	**1 + (1|ID) + (1|MY) [NULL]**	**4**	**-76.87**	**0.00**	**0.47**	NA	NA	0.22	0.40
			MO + (1|ID) + (1|MY)	5	-76.05	0.82	0.31				
			FA + (1|ID) + (1|MY)	5	-74.36	2.51	0.13				
			FA + MO + (1|ID) + (1|MY)	6	-73.52	3.35	0.09				

AICc: Akaike's Information Criterion; ΔAICc: difference in AICc compared to the best model; wi: Akaike weight

Table 3.5. Average daily path length among four neighboring groups of woolly monkeys at the Tiputini Biodiversity Station.

Group	Average	SD	Min	Max	N
Lagothrix C	1857.81	657.94	922.20	3695.43	36
Lagothrix D	2087.18	571.82	1137.98	3296.22	21
Lagothrix G	1769.20	464.59	1031.68	3130.27	36
Lagothrix P	1941.12	548.34	1193.10	2844.23	21

Table 3.6. Results of the final linear mixed models predicting the effects of group size (or subgroup size), fruit abundance, and mating opportunity index on ranging patterns. In all models, group ID and month-year were set as random effects.

Test	Response Variable	Fixed Effects	Estimate	Std. error	t value	p
Daily Path Length LMM	Daily Path Length (m)	(Intercept)	7.488	0.040	188.900	<0.001
		Mating Opportunity Index	0.146	0.039	3.728	<0.004
		Model Fit: $\chi 2= 8.249$; $p<0.005$				
Home Range Size LMM	Monthly HR size (ha)	(Intercept)	4.419	0.055	80.393	<0.001
		Social Group Size	0.148	0.052	2.866	0.044
		Model Fit: $\chi 2= 7.375$; $p<0.007$				
Core Area Size LMM	Monthly CA size (ha)	(Intercept)	3.099	0.043	71.808	<0.001
		Social Group Size	0.123	0.043	2.881	0.042
		Model Fit: $\chi 2= 6.764$; $p<0.01$				

Table 3.7. Total and monthly home range and core area sizes (ha) of four groups of woolly monkeys from August to November 2014 and April to December 2015.

	Lagothrix C				*Lagothrix D*				*Lagothrix G*				*Lagothrix P*			
	MCP		Kernel		MCP		Kernel		MCP		Kernel		MCP		Kernel	
	95%	100%	95%	50%	95%	100%	95%	50%	95%	100%	95%	50%	95%	100%	95%	50%
Total	69.8918	117.552	93.380	24.687	200.706	233.187	204.047	53.360	111.058	146.637	126.930	37.612	126.282	202.927	140.402	40.084
Aug-14	35.7071	42.000	59.473	17.794	83.5671	85.337	92.795	24.315	90.3864	101.570	122.238	31.331	35.137	39.482	62.835	14.956
Sep-14	33.1926	37.273	58.120	16.088	86.6172	92.255	113.703	33.386	42.712	67.038	72.356	15.699	45.5222	46.589	72.347	22.148
Oct-14	67.6452	76.201	100.243	25.909	149.305	162.036	168.017	43.236	63.9254	90.705	97.329	27.669	55.297	65.843	84.306	17.196
Nov-14	51.3071	56.507	79.266	23.460	56.7186	63.936	82.117	21.241	45.4376	50.813	80.313	24.673	48.447	54.504	80.293	23.950
Apr-15	48.3744	51.822	73.908	20.430	99.5298	100.850	96.147	23.674	66.5185	71.714	93.327	27.098	61.6824	64.809	86.643	19.012
May-15	34.0953	38.090	58.599	16.601	23.6351	25.029	52.355	14.568	85.0007	92.652	106.307	29.882	63.2844	72.834	90.754	25.673
Jun-15	38.8062	42.271	65.765	15.606	39.0028	46.430	65.781	14.142	78.0876	80.269	108.725	30.513	42.8003	42.973	76.179	23.501
Jul-15	47.3851	51.060	68.984	19.857	65.7536	72.822	97.826	26.510	78.5169	94.349	102.741	26.417	36.2206	39.051	62.201	17.992
Aug-15	33.1219	37.616	58.114	16.611	52.7713	74.638	85.862	23.739	71.8857	78.761	86.527	20.895	93.6035	104.428	121.530	34.575
Sep-15	25.1989	25.470	51.533	15.226	48.9705	58.218	74.439	16.892	63.169	63.377	88.113	26.373	48.8054	58.070	79.353	18.774
Oct-15	39.6492	43.340	65.602	16.692	72.9405	78.941	96.392	22.942	51.3966	57.123	81.350	25.166	96.5361	128.823	127.867	27.737
Nov-15	39.9792	47.401	67.922	18.956	74.6163	77.191	95.197	24.016	*Too*	*Few*	*Loca-*	*tions*	54.5609	57.452	88.094	21.944
Dec-15	43.9835	46.606	61.383	16.213	58.7466	80.222	95.668	29.839	65.9172	77.230	90.909	24.588	88.1245	98.611	127.944	36.552
Mean	41.419	45.820	66.839	18.419	70.167	78.300	93.561	24.500	66.913	77.134	94.186	25.859	59.232	67.190	89.257	23.385
SD	10.701	12.081	12.474	3.244	31.387	31.985	27.410	7.858	14.997	15.796	14.042	4.312	20.938	27.570	22.601	6.491

Table 3.8. Summary of monthly variation in percent home range overlap and percent core area overlap between four groups of woolly monkeys at the Tiputini Biodiversity Station, Ecuador.

			Home Range Overlap (%)				Core Area Overlap (%)			
Group Pair	Group A	Group B	Mean	St. dev	Min	Max	Mean	St. dev	Min	Max
C-D	C	D	1.30	4.51	0.00	16.28	0.00	0.00	0.00	0.00
C-D	D	C	0.79	2.72	0.00	9.83	0.00	0.00	0.00	0.00
C-G	C	G	47.93	18.87	11.06	74.19	17.80	12.51	0.00	43.96
C-G	G	C	36.92	15.86	6.34	62.09	15.66	14.17	0.00	50.00
C-P	C	P	3.55	7.88	0.00	25.31	0.00	0.00	0.00	0.00
C-P	P	C	2.38	5.76	0.00	20.20	0.00	0.00	0.00	0.00
D-G	D	G	13.56	10.84	0.00	28.30	1.90	3.05	0.00	7.57
D-G	G	D	15.92	14.96	0.00	44.42	1.89	3.52	0.00	11.38
D-P	D	P	6.90	9.08	0.00	24.58	2.95	8.52	0.00	30.56
D-P	P	D	8.83	12.79	0.00	39.07	4.34	11.16	0.00	37.93
G-P	G	P	10.85	17.29	0.00	54.29	2.25	4.70	0.00	15.00
G-P	P	G	7.17	8.98	0.00	23.40	1.41	2.87	0.00	9.42

FIGURES

Figure 3.1. Percent distribution of woolly monkey subgroup sizes among four focal groups (panels a-d) from 15-min subgroup composition (SGC) records.

a)

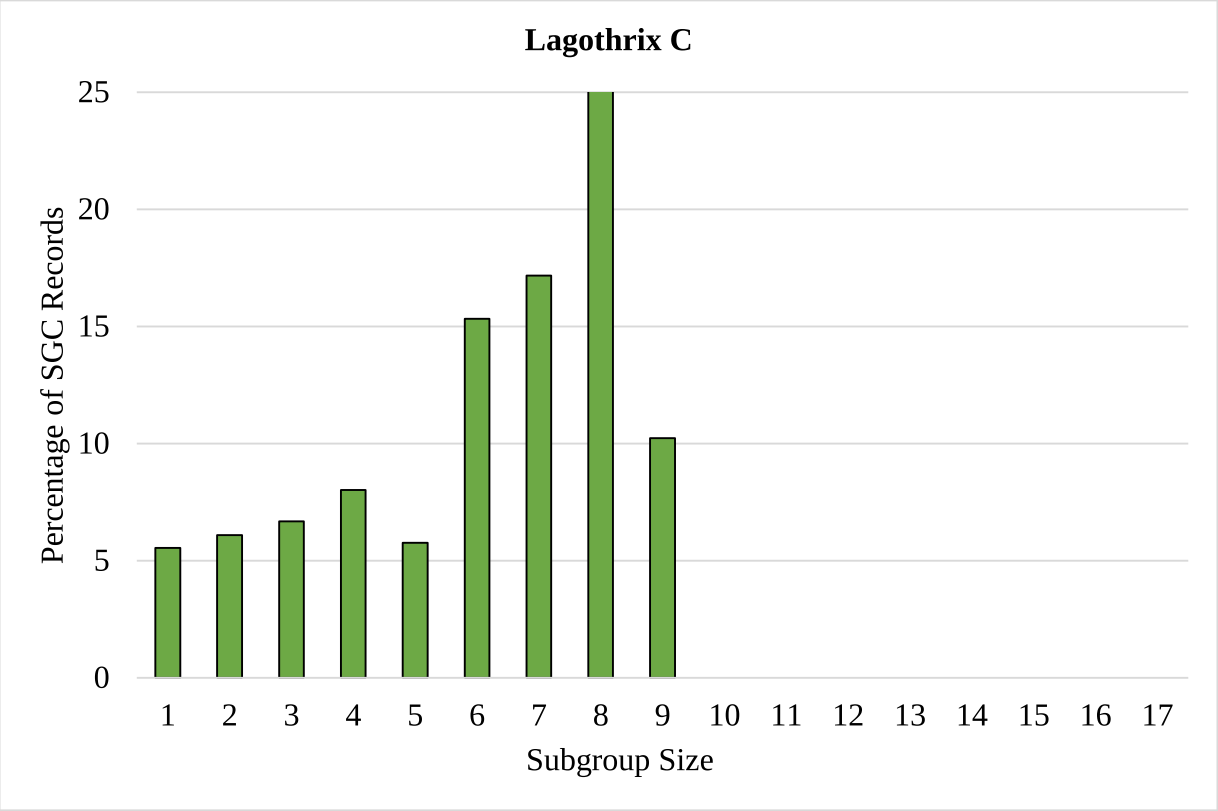


Figure 3.1 continued.

b)

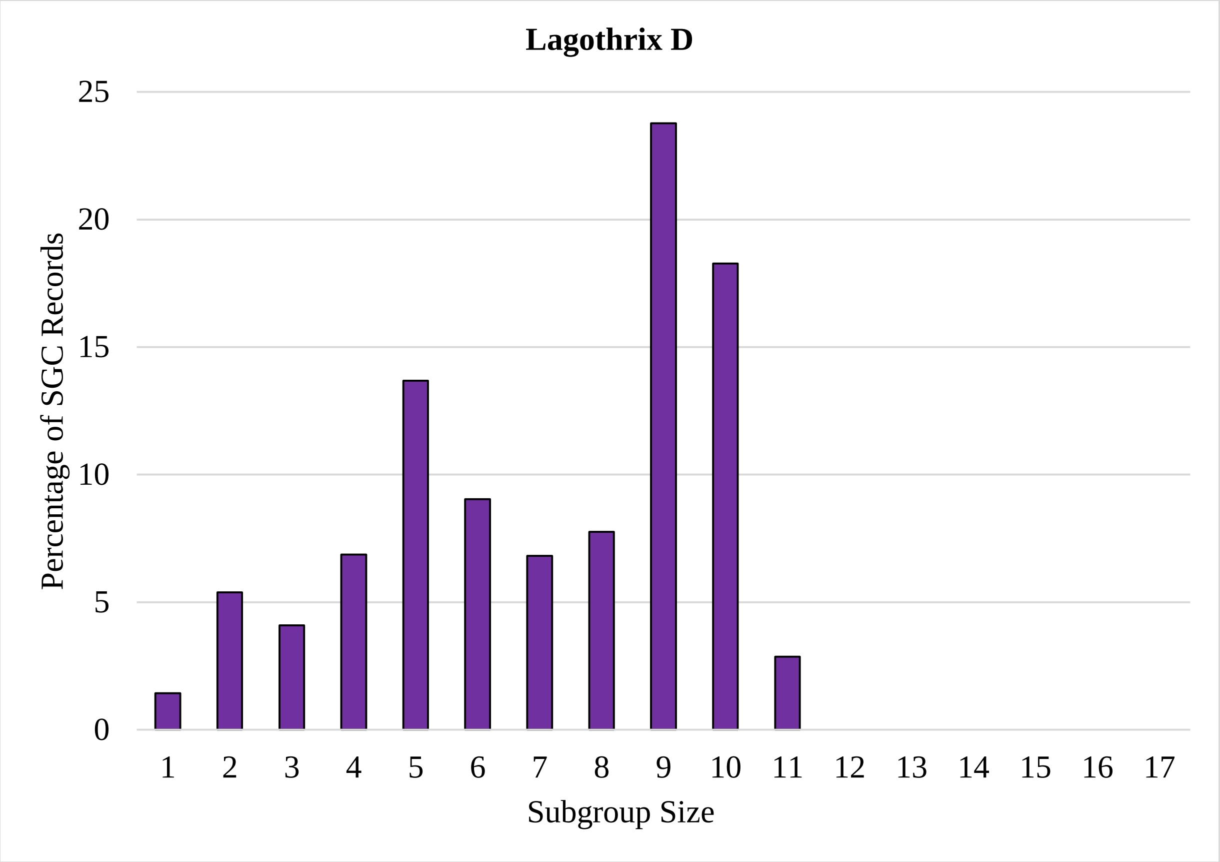


Figure 3.1 continued

c)

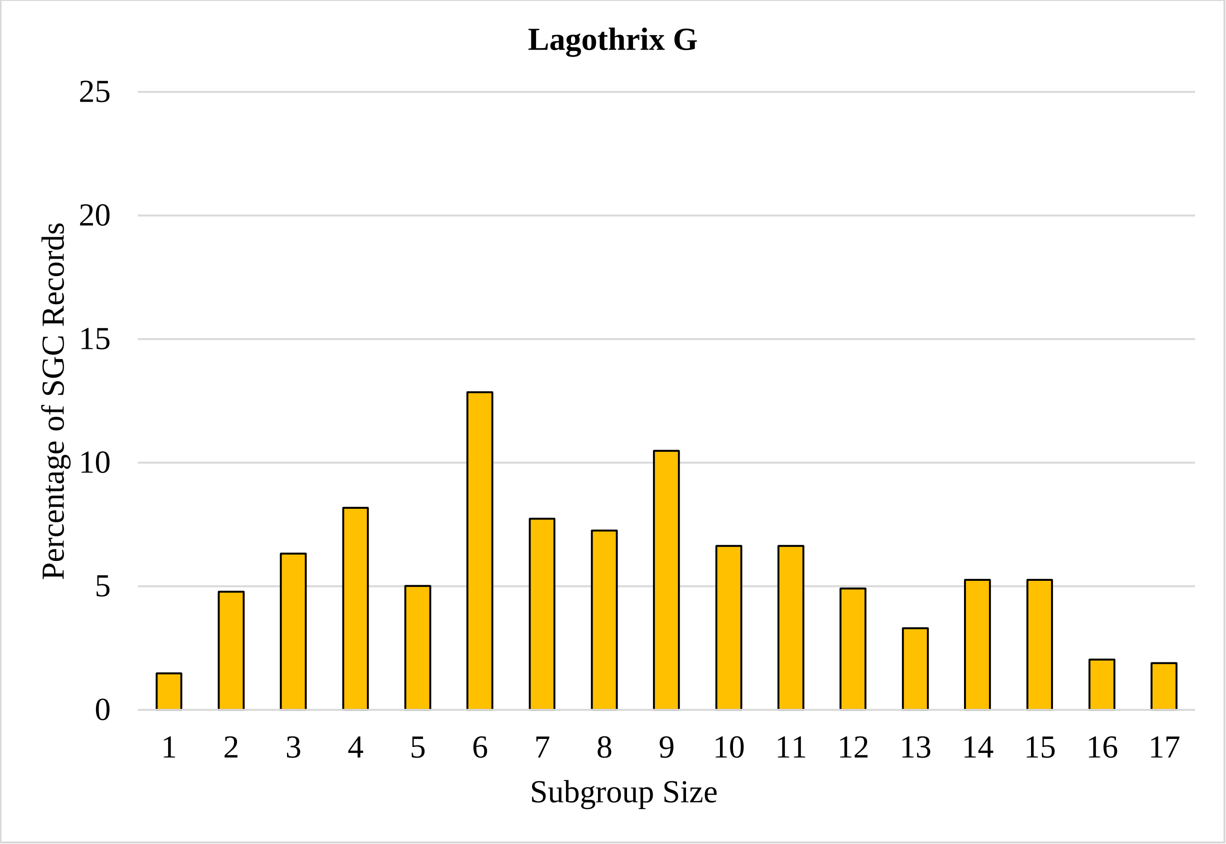


Figure 3.1 continued

d)

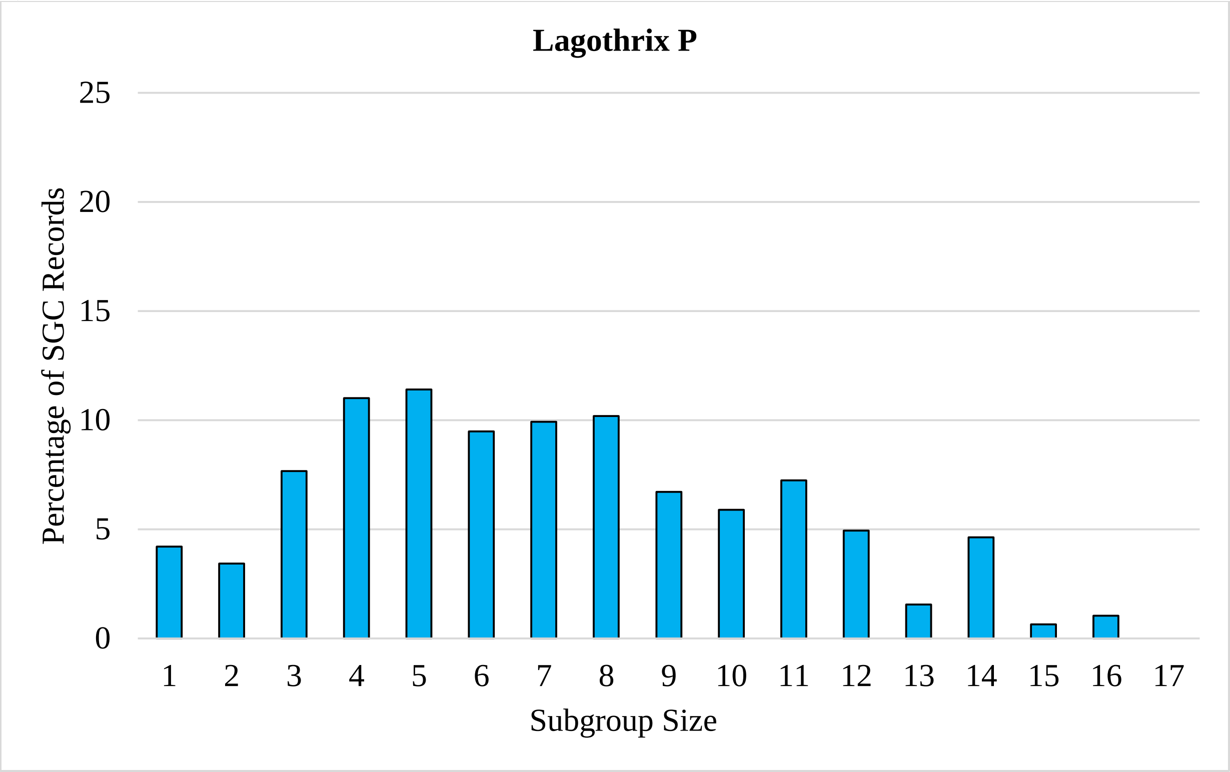


Figure 3.2. Percent distribution of distances between simultaneously followed animals from four social groups (panels a-d; N = 5,150 15-min SGC records). Dark bars represent distances between animals in the same subgroup, light bars indicate distances between animals in separate subgroups.

a)

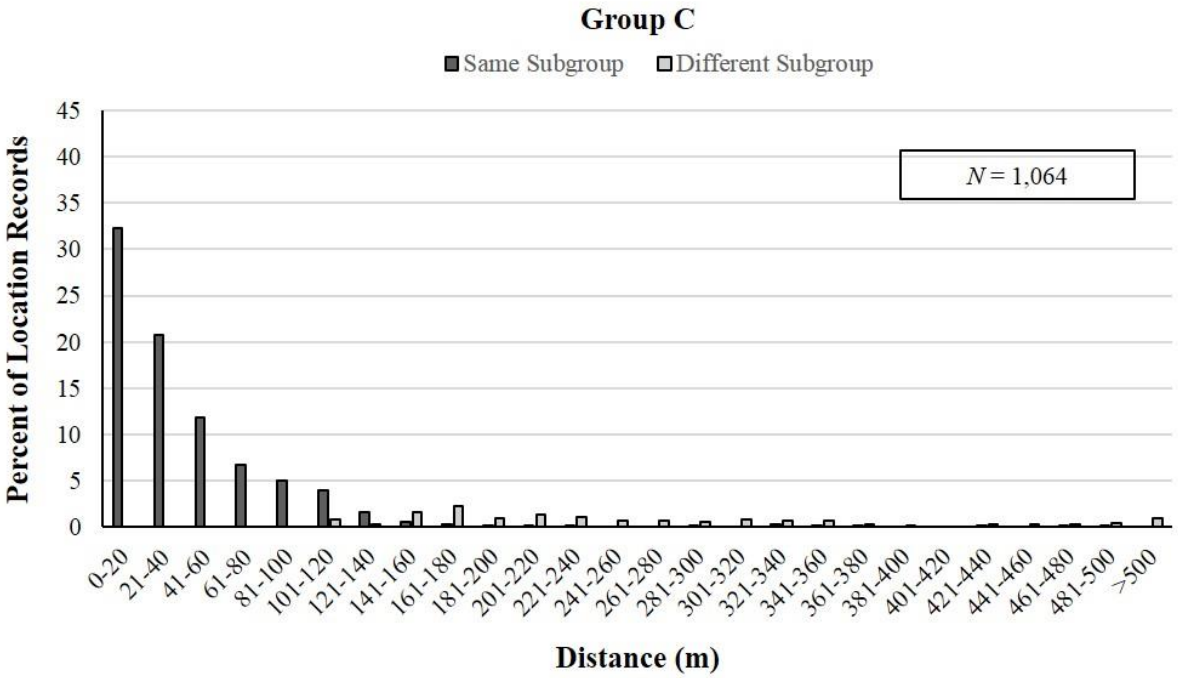


Figure 3.2 continued.

b)

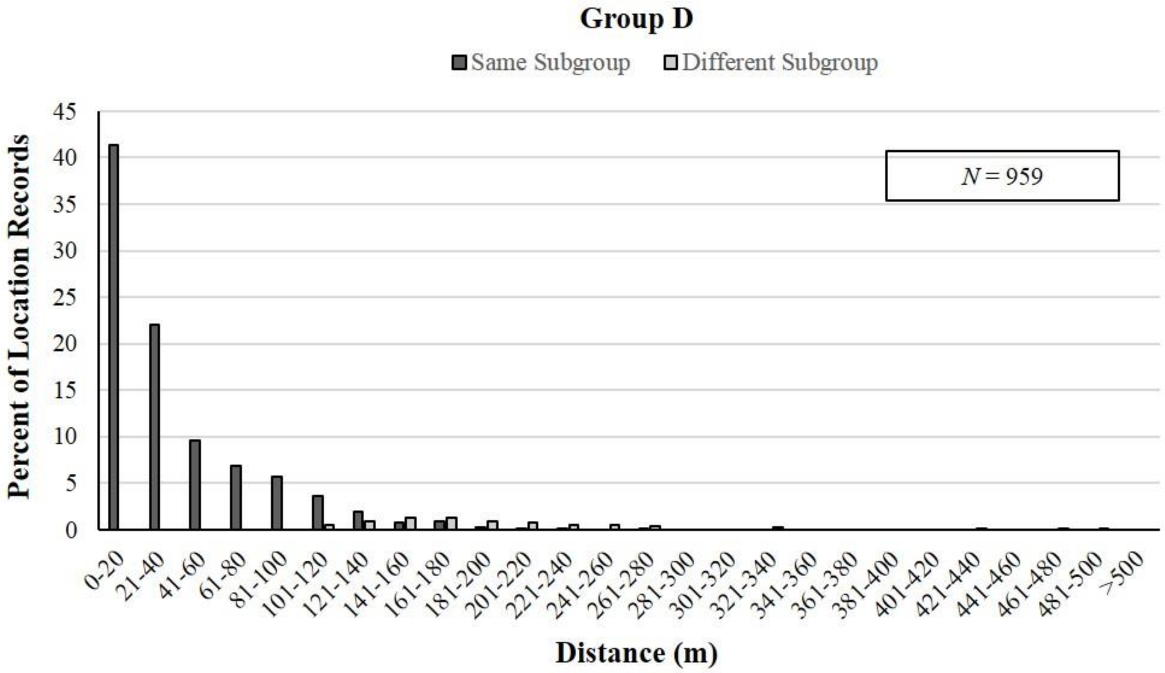


Figure 3.2 continued

c)

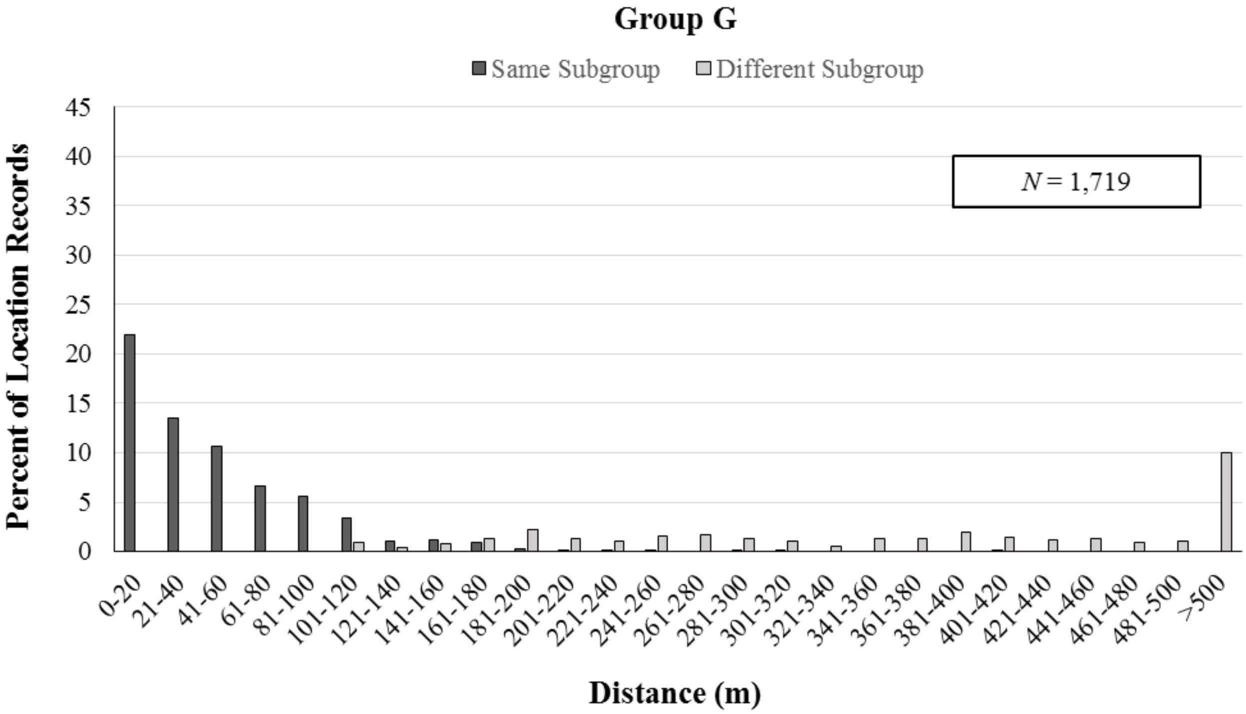


Figure 3.2. continued.

d)

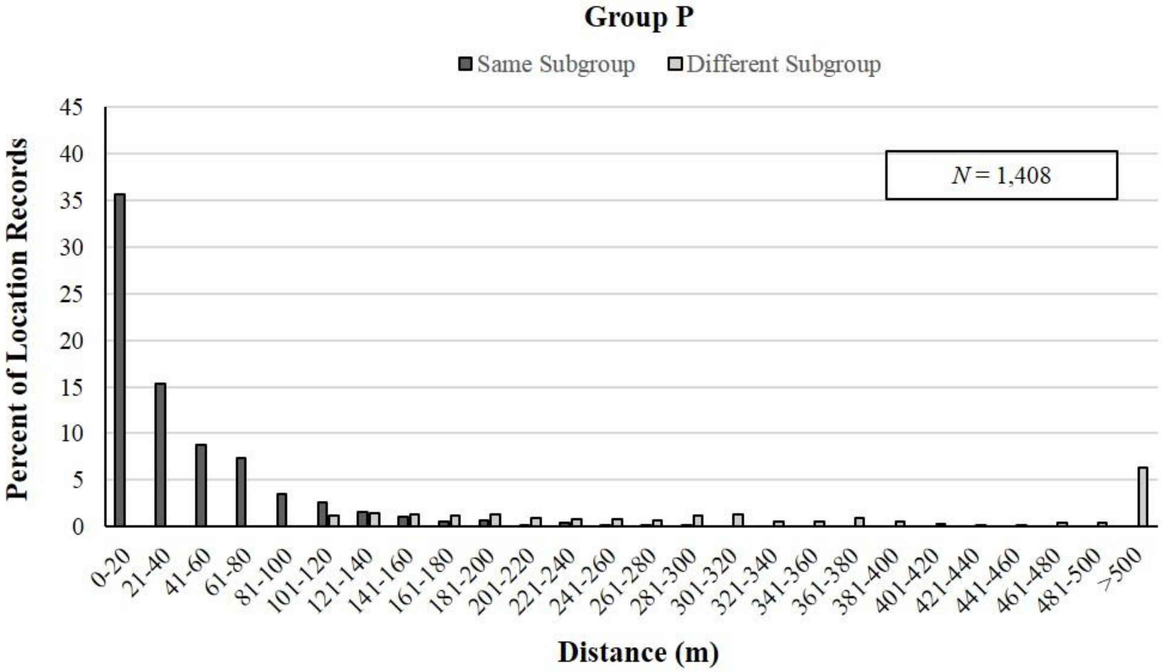


Figure 3.3. Location of home ranges (95% KDE contours), core areas (50% KDE contours), and intergroup encounters (IGEs) of four neighboring groups of woolly monkeys at the Tiputini Biodiversity Station from August 2014 to November 2014 and May 2015 to December 2015.

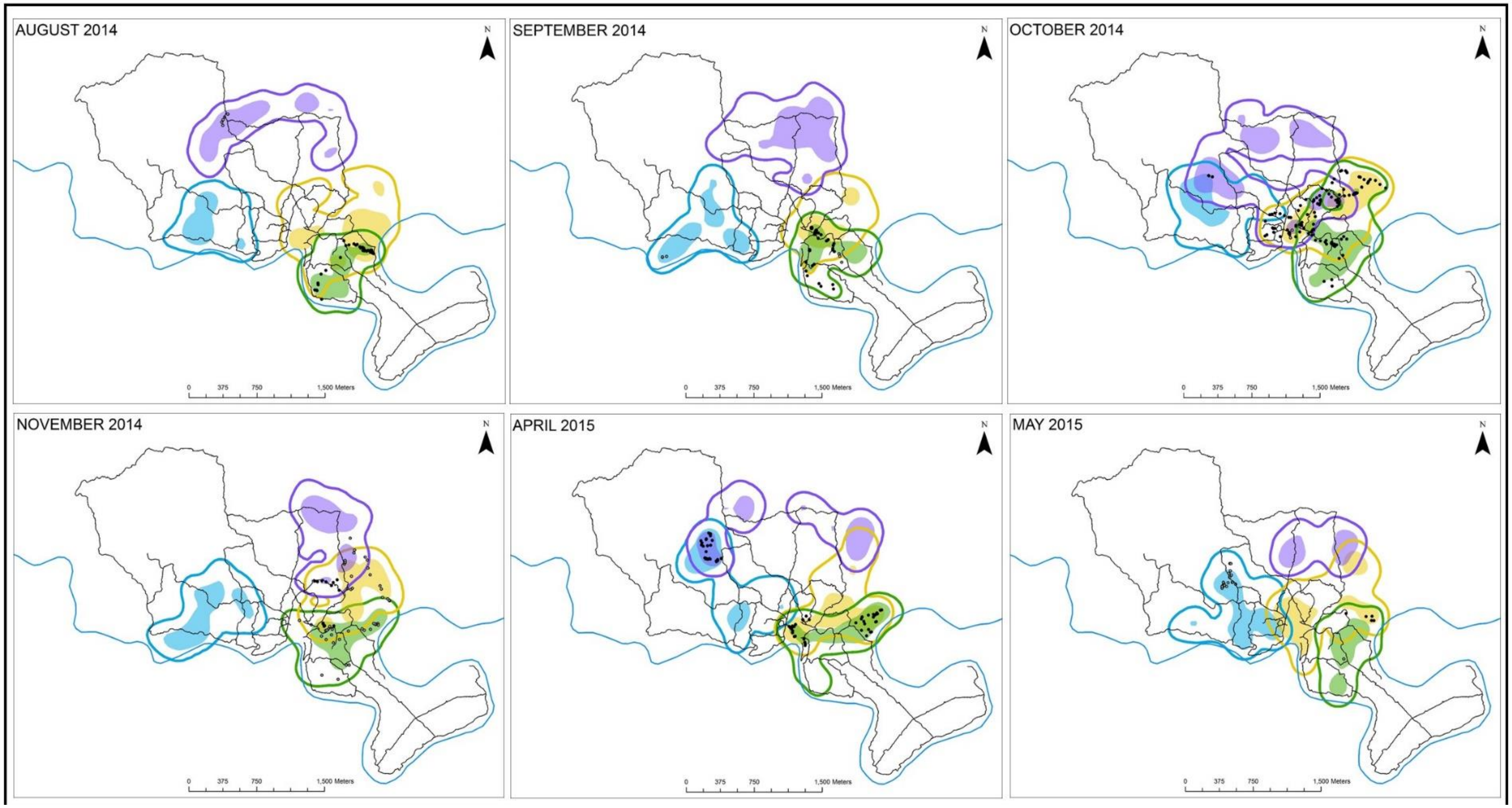


Figure 3.3 continued

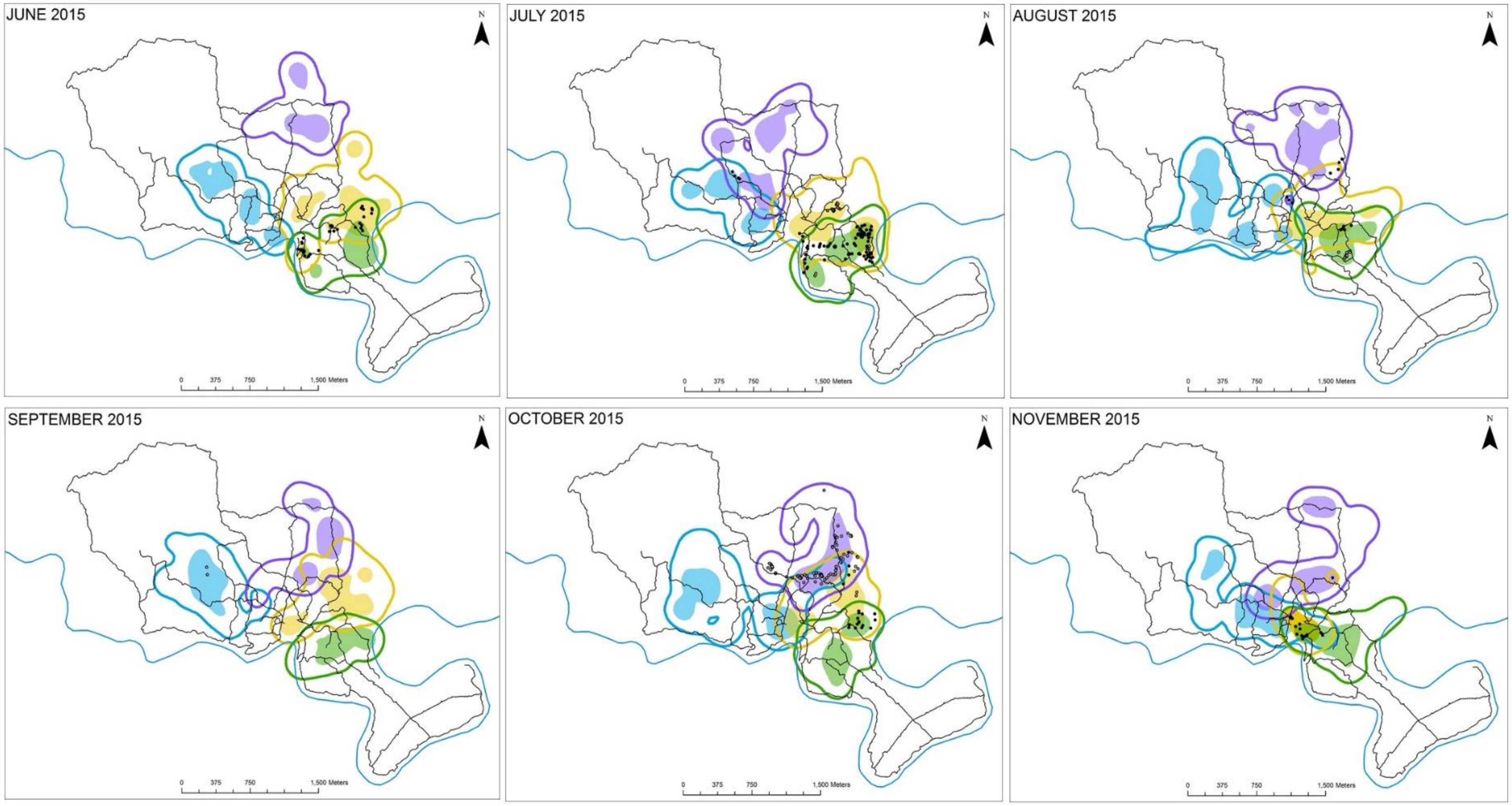
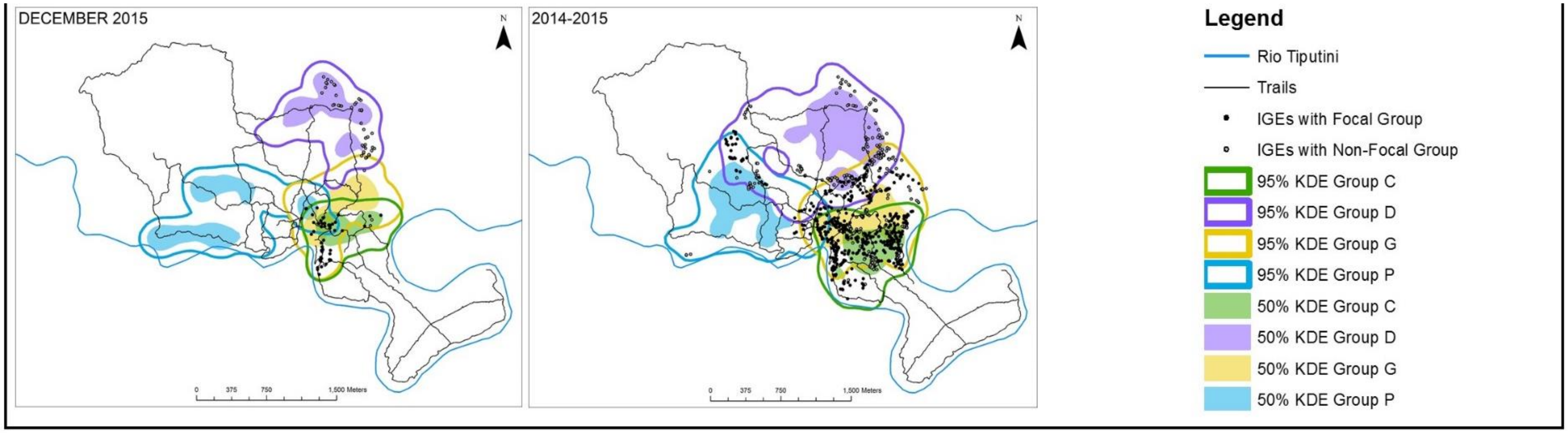


Figure 3.3. continued



Chapter 4: Social network structure and genetic relatedness among lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) at the Tiputini Biodiversity Station in Amazonian Ecuador

INTRODUCTION

When studying gregarious animals, researchers often treat individuals as “belonging to” or “members of” a particular social group. For many taxa, the social group is easy to discern, as a stable set of individuals who consistently travel, forage, and rest together in spatial proximity. In these situations, other than major demographic events (births, deaths, emigrations, and immigrations), group membership is relatively stable. However, in other cases, groups are much harder to delineate, particularly in societies characterized by high fission-fusion dynamics, where the number and identity of individuals found in sociospatial proximity changes repeatedly over time (Sundaresan et al. 2007; Whitehead 2008). For these societies, the definition of a “social group” may vary among researchers (Krause and Ruxton 2002), and what is called a group may not always be a meaningful social unit to the animals themselves (Whitehead 2008). However, the capability to accurately describe social structure – defined here as the spatiotemporal patterning of social associations among conspecifics (Hinde 1976; Kappeler and van Schaik 2002) – is imperative given that social structure can have direct impacts on an animal’s behavior and fitness (Krause et al. 2007; Sih et al. 2009; Wey et al. 2008) by influencing opportunities for mate choice, foraging and mating competition, the ability to cooperate, and the spread of information or disease (Sih et al. 2009).

A powerful tool for studying the structure and dynamics of social associations among animals is social network analysis (SNA) (Krause et al. 2007). Originally designed to characterize and explore human social interactions (Whitehead 2009), SNA can provide researcher with a visual map of selected interactions between individuals in a group or population and suggests a range of metrics that can be used to characterize overall network structure as well as the patterning of relationships among individuals within that network. Thus, SNA not only provides formal/quantitative descriptors of associations among a set of animals, but also enables researchers to test statistical models about those associations and the emergent social structure of a society (Wasserman and Faust 1994). For animal societies with fluid and flexible association patterns, social network analysis has been instrumental in uncovering more subtle grouping dynamics and social tiers within a population (e.g., geladas [Mac Carron and Dunbar 2016], Guinea baboons [Patzelt et al. 2014], reticulated giraffes [Carter et al. 2013]) as well as differences in the patterning of associations among individuals in closely-related species previously thought to share similar social structures (e.g., African savanna elephants and Asian elephants [de Silva and Wittemyer 2012], onagers and Grevy's zebras [Rubenstein et al. 2015]).

In this chapter, we use SNA to explore spatial associations and emergent social structure in a population of wild woolly monkeys (*Lagothrix lagotricha poeppigii*) from the Tiputini Biodiversity Station in lowland Ecuador. Woolly monkeys make a particularly interesting case study for the application of social network analysis because patterns of association (i.e., namely temporal and spatial cohesion) among individuals both within and between the putative social groups recognized by observers have been characterized differently over time and across populations. For example, some researchers have described woolly monkeys as living in large, discrete, multimale-multifemale social groups that remain relatively cohesive throughout the day (Di Fiore 1997; Nishimura 1990, 1994; Peres 1996), while others have noted that social groups sometimes split into temporary subgroups that range independently from one another but still maintain intermittent contact (Ramirez 1980; Ramirez 1988; Soini 1986; Defler 1996; Di Fiore 1997). Others still have suggested that woolly monkeys live in fluid societies characterized by highly flexible and dynamic patterns of intragroup associations, similar to those characterizing spider monkeys and chimpanzees (Kavanagh and Dresdale 1975). While current consensus posits that woolly monkeys live in relatively cohesive social groups that occasionally fission into tightly-grouped feeding parties and/or coordinated subgroups that can persist for several hours or even days (Defler 1996; Di Fiore 1997), few studies have explicitly explored such dynamics (but see Chapter 3; Ellis and Di Fiore in press; Peres 1996).

Moreover, some long-term field studies of woolly monkeys have suggested that not only do putative social groups sometimes fission into parties or subgroups comprising a subset of group members, but also that the members of two or more putative social groups may coalesce in overlapping areas of their respective home ranges to form large aggregations, sometimes referred to as “supergroups,” that rest, travel, and forage together without overt aggressive interactions for up to several hours (Defler 1996; Di Fiore 1997; Di Fiore et al. 2009; Nishimura 1990; Peres 1994). Additionally, subsets of individuals from neighboring social groups have been observed to form independent parties that associate and range apart from other members of their respective social groups (Chapter 3; Ellis and Di Fiore in press), and solitary individuals are known to occasionally visit other social groups for several hours or days without apparent conflict (Nishimura 1990; Nishimura 2003). Yet again, to our knowledge, no study has quantitatively examined if association patterns among individuals within and between putative social groups are stable and predictable (i.e., do subgroups formed by individuals from the same social group or do aggregations of individuals from different social groups consistently comprise the same sets of individuals). If so, such a social structure would contrast with the “individualistic” fission-fusion dynamics of spider monkeys and chimpanzees and be more akin to the “molecular” fission-fusion dynamics of elephants, geladas, hamadryas baboons, and some colobines (Kappeler and van Schaik 2002) which live in multilevel societies. Table 4.1 provides an overview of a number of terms introduced above and used in the remainder of this chapter for describing the social structures of taxa, like woolly monkeys, with highly fluid social association patterns.

Furthermore, although woolly monkeys are often considered to live in male philopatric groups, prior genetic work on one population has revealed that many adults of both sexes have at least one other adult resident in their current social group who is estimated to be a close relative (i.e., a parent, an adult offspring, a full sibling, or a half sibling: Di Fiore and Fleischer 2005, Di Fiore et al. 2009) and may have both same- and opposite-sex adult kin residing in neighboring groups as well, implying a strong potential for kin-biased affiliative behaviors not just within but also between groups. Individuals that preferentially associate with kin may receive indirect fitness benefits (Hamilton 1964). Among primates, cooperative behavior among female kin, such as allomothering or coalitionary support to prevent other females from immigrating into their group, has been shown to increase female fitness through enhanced reproductive success (e.g., Pope 1990; Pope 2000a; Silk 2007; Silk et al. 2009). Affiliative and cooperative behaviors tend to be rarer among males in many group-living primates, but such behaviors have been documented in several species characterized by male philopatry, such as chimpanzees (Mitani 2009) and spider monkeys (Aureli et al. 2006), most often in the form of territorial defense. Moreover, in the bisexually dispersing ursine howler monkey, males that reside and form coalitions with male kin enjoy longer tenure and higher reproductive success (Pope 1990; Pope 2000b). In only a few primate societies do individuals appear to seek out or preferentially associate with opposite-sex kin (e.g., bonobos, Hohmann et al. 1999), but potential benefits of such intersexual nepotism may include lower levels of sexual coercion and harassment of females by males, reduced risk of infanticide, more effective resource defense or defense against predators, and sharing of social and ecological knowledge (Wiszniewski et al. 2010). Persistent association with opposite sex relatives in mixed sex parties has also been hypothesized to increase an individual’s familiarity with potential mating partners, who are affiliates of those kin (Möller et al. 2006). Kin associations may also increase the levels of social cohesion and/or reduce levels of conflict between social groups. For example, social groups of African elephants are more likely to coalesce with members of other social groups that contain related matriarchs or females from the same maternal lineage (Archie et al. 2006). Similarly, among western gorillas, peaceful intergroup associations have been attributed to a dispersed network of male kin, where leading males of adjacent social groups are genetically related (Bradley et al. 2004).

While several studies have investigated spatial associations and affiliative tendencies across age and sex classes in woolly monkeys (Di Fiore and Fleischer, 2005; Stevenson 1998; Nishimura 1990, 1994) and have examined the degree of relatedness among males and females within and between social groups (Di Fiore and Fleischer 2005; Di Fiore et al. 2009), it remains unclear to what extent genetic relatedness influences the association patterns of individuals both within and between social groups. To fill this gap, we coupled behavioral data with social network analysis and molecular techniques to examine association patterns among a large set of individually-recognized woolly monkeys from multiple putative social groups. Specifically, we used association data collected at two spatial scales (party membership and close spatial proximity) from more than 50 adults and subadults over two four-month study periods 1) to identify natural grouping patterns of woolly monkeys and determine if subgroups and/or parties of individuals from different social groups are repeatedly composed of the same sets of individuals (which could indicate the existence of meaningful social units beyond that of the social group) and 2) to assess how genetic relatedness maps on to the strength of associations among individuals within and between identified groups. If woolly monkeys gain inclusive benefits from associating with kin, as demonstrated in other group-living taxa, then we predict that highly related individuals (i.e., those with parent-offspring or full- or half-sibling relationships) from the same social group will have higher rates of association than non-related individuals.

Given that the two study periods correspond to different epochs in the seasonal reproductive cycle of woolly monkeys (see Chapter 2 and Ellis et al. in revision), further predictions may be made about the association patterns of same-sex kin. The first study period (August 2014-November 2014) corresponds to a time in which females begin actively soliciting males for copulation, with conceptions occurring in the latter two months of this period for a large number of females. Males were predicted to associate more often with male kin during this period, as male-male coalitions may improve reproductive success when more reproductively active females are present. The second study period (May 2015-August 2015) corresponds to the birthing season, when a majority of infants are born and/or females near parturition. We predicted that female kin would be more apt to associate with one another during this period, as, when more infants are present, cooperative behavior among female kin may help reduce infanticide risk and facilitate infant rearing (although it should be noted that infanticide has never been observed in wild woolly monkeys).

METHODS

Study Site

This study was conducted at the Tiputini Biodiversity Station (TBS) in lowland Ecuador (Fig. 4.1). Located within the Yasuní Biosphere Reserve, the station is situated in one of the largest remaining tracts of primary lowland rainforest in Western Amazonia. Over 30 km of well-marked trails provide access to nearly 650 ha of *terra firme* and seasonally flooded forest. Rainfall in the region generally exceeds 2800 mm per year (Blake et al. 2010; Di Fiore et al. 2009). While there is not a pronounced dry season, rainfall can vary dramatically between months, with March through July often found to be the wettest months of the year, averaging >250 mm of rain per month. Fruit availability also varies throughout the year, with the highest abundance of ripe fruit typically found between January and March and the lowest abundance of fruit observed between July and August (Link et al. in preparation). The field site is host to 10 different primate species, including three atelines (*Ateles belzebuth*, *Lagothrix lagotricha poeppigii*, and *Alouatta seniculus*), and boasts an intact predator community (Blake et al. 2012).

Study Population

At least eight putative woolly monkey social groups are known to range, either wholly or partially, within the TBS trail system (Fig. 4.1). These groups vary in size from 13-40 individuals, with typical composition including 2-5 adult males, 4-10 adult females, and 5 or more immatures. Since 2006, at least one animal from each of these putative social groups has been captured via remote intramuscular injection of ketamine HCl or a reconstituted mixture of tiletamine HCl and zolazepam HCl (Zoletil®) using a CO_2-powered rifle and then fitted with a Telonics™ or Holohil™ VHF transmitting radio-collar to facilitate the location and tracking of the animals and those they associate with. During processing, researchers collected morphometric data (e.g., weight, body length, limb length, testicle size, dental wear), swabs of the pectoral and anogenital regions, and a tissue biopsy to serve as a source of high-quality DNA. All anesthetization procedures adhered to protocols reviewed by the Institutional Animal Care and Use Committee at the University of Texas at Austin (Protocol Numbers AUP-2011-00157 and AUP-2014-00412) or, prior to 2011, at New York University and were approved by the Ecuadorian Ministry of the Environment. Intermittent monitoring of the woolly monkeys began in 2006, with observational data being taken on three of the putative social groups (D, G, and I) between 2007 and 2009, on two of the putative groups (C and G) in 2013, and on four of the putative groups (C, D, G, and P) from 2014 to the present. For the current study, we only considered a subset of behavioral data collected between 2014 and 2015, and genetic samples collected between 2013 and 2017.

Behavioral Data Collection

Behavioral and ranging data on animals from putative social groups C, D, G, and P were collected by KME and a total of seven field assistants over two field seasons (May 2014-December 2014 and April 2015-December 2015). KME personally trained all field assistants in animal recognition and data collection protocols. Data collected during focal animal samples, detailed below, were not included in analyses until KME and assistants had completed eight weeks of training in 2014 and six weeks of training in 2015. The longer duration of training in

2014 was due to the need for KME and assistants to learn the ranging habits and individual IDs of animals belonging to study groups D and P, as these animals had not been previously followed by KME, whereas in 2015 animals in all four social groups, with the exception of newly immigrated animals, were already known by KME thus expediting the training process. An exception to this extensive training period was made for two assistants during the summer of 2015; because these assistants were only tasked with following primarily group C, a small group, their focal data for that group was incorporated after only two and a half weeks of training, following demonstrated accuracy with identifications and other aspects of data collection.

After initial training, interobserver reliability was assessed at the beginning of each month, when KME and all assistants went to the field concurrently and collected data on the same group. During these sessions, observers came to consensus on estimated distances between individuals (corroborated with a handheld range finder and trail markers spaced 25 m apart), coding of behaviors, and animal identities. At no time during interobserver reliability checks did observers assign different identities to individuals in question.

Between 2014 and 2015, each putative social group under study had one to two animals that were fitted with functioning radio-collars. Animals were individually recognized by the presence of radio-collars with identification tags (functioning and non-functioning), facial scarring, variation in pelage color, broken digits, and/or differences in anogenital size and pigmentation. Individual identities were further corroborated between field seasons through genetic recapture (Di Fiore et al. 2009), and observers were requested, to the best of their ability, to collect feces from any animals whose field-assigned identity was uncertain. Age-sex categories were determined based on external morphology and behavior as described in Schmitt and Di Fiore (2014). We differentiated between adult females with dependent offspring (i.e., infants and juveniles that were usually under approximately two years of age and were either carried by or were in clear association with the female) and adult females with no dependents, which were either nulliparous females or females that were no longer encumbered by a dependent offspring (i.e., juveniles that were usually over 2 years of age and locomoted independently). For parous females, this differentiation marked the period during which mothers were most likely to return to sexual activity and successfully conceive (see Chapter 2). Given the stark variation in body size and secondary sexual characteristics among adult males, we also classified males into two categories: big adult males (BAMs) and small adult males (SAMs). Big adult males were differentiated from small adult males by their larger size, bulky morphology, and marked development of other secondary sexual characteristics, including the presence of long, dark, and often greasy fur along the midline of their chests, large temporal muscles that create well-defined crests, large and pendulous testes, and a scrotum covered with a long, conspicuous tuft of fur. While smaller adult males were observed to have some development of these secondary sexual characteristics, such as darkening of the chest fur near the midline and variable growth of the scrotal tuft, these characteristics were much more exaggerated in BAMs. The total number of adults plus subadults in the four study groups varied between ~8 and ~19 individuals, with total group size, including juveniles and infants, ranging from ~14 to ~30 individuals (Table 4.2). Typically, groups contained 1-2 BAMs, 2-3 SAMs, and 5-10 adult females.

Behavioral data were recorded using a combination of instantaneous and continuous sampling in the context of day-long focal follows (Altmann 1974). Due to the high degree of fission-fusion dynamics that characterizes woolly monkey social organization (see Chapter 3; Ellis and Di Fiore in press), we were unable to follow a strict rotating schedule of predetermined focal animals. Instead, we targeted a pre-arranged social group for sampling each day, and once individuals attributed to that group were located, observers opportunistically selected a focal subject to follow, giving preference to those adult or subadult individuals with the fewest number of accumulated observation hours for that given month. When observers outnumbered the pool of eligible focal animals in a subgroup, extraneous observers were tasked with searching the assigned social group's home range for eligible animals in other subgroups. During focal animal follows, the behavior of the focal individual, and the identity and/or age-sex class, behavior, and distance of the focal animal's nearest neighbor were recorded instantaneously every 5 minutes, as well as the identity and/or age-sex class and distance category (contact, 0 to 1 m, 1 to 5 m, 5 to 10 m) of all animals within a 10 m radius. Feeding behavior and social interactions were recorded continuously. Rare events such as mating behaviors (e.g., copulations, mating solicitations) between non-focal individuals were recorded *ad libitum*.

Party Composition Records

Following the "gambit of the group" (GoG) method (Whitehead and Dufault 1999) for describing party composition, observers noted the identity and/or age-sex class of all animals their focal individual was associated with every 15 minutes (on the hour and at 15, 30, and 45 minutes after the hour) and recorded the general activity of the majority of those individuals ('Resting', 'Moving', 'Foraging', 'Socializing'), the location (using a handheld GPS unit [Garmin 76CSx or GPSMap64]) of the center of mass of that set of animals, and an estimate of spread (i.e., the distance, in meters, between the farthest two members of the set). This technique coarsely assumes that all individuals seen "clustered" or "grouped" together during a sampling period are associating with every other individual in that "cluster" or "group" (Franks et al.

2010). In other studies, criteria for who is considered “grouped” often rely on measures of spatiotemporal proximity (i.e., animals that are found within so many meters of one another, within a specified amount of time), using cutoffs that are presumed to be biologically relevant for the animals in question (Croft et al. 2008). Here, we considered animals to be associating in the same party when they maintained visual or low intensity vocal contact with one another 15 minutes before, during, or after each sampling period (Bezanson et al. 2008; Chapman et al. 1995) and were located at a distance of no more than 100 m from at least one other party member following a chain rule (e.g., Ramos-Fernández 2005). Post-hoc analyses investigating the distribution of interindividual distances among simultaneously followed animals verified that this was an appropriate measure with association patterns becoming qualitatively and quantitatively different from close spatial associations at roughly 80-130 m, depending on group size (Fig 4.2). The GoG approach has been an important method for evaluating social structure in animals with fission-fusion dynamics, particularly those for which individual identification may be incomplete and/or social interactions among individuals may be difficult to observe (Farine and Whitehead 2015; Whitehead 2008).

Observers following animals “grouped” together were able to communicate using two-way walkie-talkie radios to inform one another about their focal subjects’ relative positions, as well as about the arrival and departure of other individuals from the group. Party assignments were further corroborated through telemetry checks in which observers scanned the vicinity for radio-collared animals belonging to any of the four study groups and with post-hoc analyses confirming spatial distances between observers and the animals they were following (see Chapter 3; Ellis and Di Fiore in press). Adults and subadults from the four study groups were followed from dawn to dusk (circa 06:00 – 18:00) on a rotating schedule, with observers contacting each group on average 4-8 times per month (range: 3-19 days), contingent upon weather and the number of eligible focal individuals in each group. A summary of focal hours for individual animals followed throughout the study appears in Table 4.3.

Characterizing Patterns of Association and Social Networks

Animals that were followed as focal animals but were not recorded as present in all four months of data collection used for each respective field season were excluded from social network analyses (N = 2 adult females in 2014 and N = 2 adult females in 2015), leaving a total of N=52 adult and subadult animals spread among the four study groups. We then measured association patterns at two spatial scales: association in the same party and association in close spatial proximity (<5 m). The strength of dyadic associations based on presence in the same party was calculated using the simple ratio index (SRI), defined here as the number of sampling periods in which both animals were observed in the same party divided by the total number of sampling periods in which either animal was observed (Cairns and Schwager 1987). Simple ratio indices were calculated in SocProg 2.8 (Whitehead 2009) with sampling periods set to an interval of four hours to reduce autocorrelation among the set of party composition records. The total number of independent records used to calculate SRIs was 8,302, with 3,603 of those records collected in 2014 and 4,699 of those records collected in 2015. Individual focal animals included in network analyses appeared in party composition records an average of 474±169 times in 2014 and 636±204 times in 2015.

Proximity-based association indices (PAI) were calculated for each dyad as the proportion of 5-minute sampling points that the pair was observed in close spatial proximity (0 to 5 m) of one another divided by the total sum of such proximity records collected on both individuals while in view during focal follows. Due to the occasional difficulty of locating animals, particularly for our larger groups, focal animal sampling was biased towards radio-collared animals. Furthermore, in summer 2015, an auxiliary project focused on collecting focal data on females from Group C, consequently inflating the total number of focal hours available for that group during this time period. Thus, to correct for unequal sample sizes across focal animals, we constructed proximity-based association indices using a subset of the data as follows. We first removed, for each four-month sampling period, all adults and subadults with fewer than 72 proximity records in the dataset (N = 1 small adult male, 8 adult females, and 2 subadult females in 2014 and N = 2 subadult females in 2015), leaving only those with > 6 hours of focal observation time in each respective period. Then, we also restricted the number of proximity records analyzed for each focal animal to 100 per month (i.e., 8.33 hours). We chose this cutoff as it represented the average number of instantaneous records collected each month on non-collared animals while also excluding the inflated hours of group C females in 2015. For those individuals with > 100 instantaneous records collected in a given month, we randomly subsampled 100 records using a custom function written in R version 3.3 (R Core Development Team). This procedure resulted in a total dataset of 8,065 instantaneous samples for 39 individuals in 2014 and 12,516 instantaneous samples for 49 individuals in 2015, with an average of 231.2±89.5 samples per individual, or 19.3±7.5 hours, per field season, which were then used to construct PAI based networks. We repeated this entire random selection process and subsequent network construction ten times to evaluate the robustness of the network structure to changes in the particular subsample used to construct it.

Network Visualization and Analysis of Social Structure

We used Gephi 3.0 (Bastian et al. 2009) to visualize woolly monkey social networks based on SRI and PAI matrices for each field season, and we used indices of network modularity and hierarchical cluster analysis, calculated in SOCPROG 2.8 (Whitehead 2009), to evaluate the extent to which the social structure of woolly monkeys comprises multiple clusters of individuals and if those clusters (or “social units”) can be organized into discernable hierarchical levels. We first evaluated network modularity using Newman's (2006) eigenvector-based clustering method, which finds the most appropriate way to divide a network into n-clusters based on network topology by finding subsets of individuals that have more connections to one another than to those outside of their subset (Girvan and Newman 2002), without assuming a hierarchical structure between individuals. Conceptually, network modularity indicates how well a sample of individuals can be separated into distinct “social units” (Whitehead 2008). Maximum modularity, referred to as ‘Q’, scores range from 0.0 to 1.0, with 0.0 indicating a completely random association of individuals, and 1.0 indicating no associations between individuals in different, closed social units. Conventionally, Q scores of 0.3 or higher are taken to indicate the presence of important divisions among sampled individuals (Newman 2004). To further determine if substructure existed within identified clusters, we ran the eigenvector-based clustering method again, but this time applied to each cluster individually (*cf.* Tavares et al. 2017).

For the hierarchical cluster analysis, associations were rendered as bifurcating dendrograms using several available methods (the average linkage method, Ward’s weighted method, the complete linkage method, and the single linkage method). Resulting dendrograms were then compared to the SRI and PAI association matrices using the co-phenetic correlation coefficient (CCC), where coefficients of > 0.8 indicate a good fit between the dendrogram and the matrix of association scores (Sokal and Rohlf 1962). Of the clustering methods tested, the average linkage method provided the highest CCC value across all matrices (range: 0.896-0.989) and was thus used for all subsequent hierarchical cluster analyses. To determine if individuals could be divided into distinct social tiers we first tested the modularity of the network using "modularity-G" which finds the association index that maximizes modularity within the network while controlling for gregariousness, or the tendency to associate, across individuals (Newman 2004; Whitehead 2008; Whitehead 2009). In this context, modularity is the difference between the proportion of the total associations within clusters compared to the expected proportion (Whitehead 2008), where the expected proportion for *modularity-G* is calculated by dividing the association index between animal A and B by the sum of all association indices involving animal A and all of the association indices involving animal B, then multiplying by the sum of all of the association indices across the network (Godde et al. 2013; Whitehead 2009). We evaluated whether association indices were significantly higher among individuals identified as belonging to the same cluster on the bifurcating tree compared to those from different clusters using Mantel tests. In addition to *modularity-G*, we examined graphs that plotted for each dendrogram the cumulative number of bifurcations (or branching events) as association indices increased over the network (Whitehead 2008; Wittemyer et al. 2005). The points where the changes in the slope of bifurcation rates are significantly different above versus below that point are termed knots and may be used to identify cut-off values between social tiers. Following Wittemyer et al. (2005) and Snyder-Mackler et al. (2012), we identified the knot that maximized this rate of change by comparing the distribution of bifurcations per step-wise increment (0.05 for dendrograms constructed from SRI values, and 0.01 for dendrograms constructed from PAI values) above versus below each potential knot using the Wilcoxon rank-sum test.

Genetic Sample Collection and Molecular Analyses

Biological samples used for molecular analyses (N = 228) were collected between May 2013 and July 2017 from individuals belonging to seven of the eight putative social groups that occupy the TBS trail system. A majority of these genetic samples (N = 211) were collected opportunistically and non-invasively from individuals immediately after defecation. The remainder of the samples (N = 17) came from individuals that were captured following procedures previously described. During processing, a small (2-3 mm) tissue biopsy punch was taken from the ear of each individual as a source of high-quality DNA. All biological samples were placed in a nucleic acid preservation buffer (either commercially purchased RNALater [Ambion] or a homemade alternative (Camacho-Sanchez et al. 2013) at a volume ratio of ~2x buffer:1x sample and then stored at room temperature for up to 6 months prior to transportation to the Primate Molecular Ecology and Evolution Laboratory at the University of Texas at Austin for DNA extraction and multilocus genotyping.

Genomic DNA was extracted using either Qiagen DNeasy Blood and Tissue Kits or QIAamp Stool Mini Kits, for tissue and fecal samples, respectively. For both kits, we followed the extraction protocol recommended by the manufacturer, making the following slight modifications to the stool extraction procedure: 1) samples were left to lyse in ASL buffer at 56^0C in a thermal mixer for 12-24 hours, 2) samples were incubated with proteinase K and buffer AL at 70^0C for 30 minutes, agitating them every 10 minutes, and 3) extracted DNA was eluted from spin columns using 100 μl of buffer AE that had been heated to 70^0C after sitting in the membrane at room temperature for 30 minutes.

Individuals were genotyped at a total of up to 12 microsatellite loci using a combination of primers either isolated from woolly monkeys or isolated from other primates and found to be highly variable in *Lagothrix* (Table 4.4; Di Fiore and Fleischer 2004; Di Fiore et al. 2009) or other atelines (Cortés-Ortiz et al. 2010; Gonçalves et al. 2004). Polymerase chain reaction (PCR) amplifications for each locus were completed in a total volume of 5 μl consisting of 2.5 μl of 2X Qiagen Multiplex PCR master mix, 0.07 to 0.11 μM each of forward and reverse primers, and 1.5 μl of unquantified DNA template from original extraction elutions. For each locus, either the forward or reverse primer was labeled with a fluorescent dye (6-FAM, HEX, or NED; Applied Biosystems). Each PCR contained either a single locus or a multiplexed set of 2-3 loci that varied in target amplicon size and fluorophore. Following denaturation of the DNA template, PCR amplifications for each marker locus were carried out for 37 cycles with an annealing temperature of 55^0C. PCR products were mixed with GeneScan 500-ROX size standard and submitted to the DNA Sequencing Core Facility at the University of Texas at Austin for separation and visualization on an ABI 3130XL DNA Analyzer. Allele sizes were determined using GeneMapper 4.0 software (Applied Biosystems). Genotyping was carried out using a modified version of the multiple tubes approach (Taberlet et al. 1996; Di Fiore et al. 2009). To minimize genotyping errors due to allelic dropout, we verified heterozygous genotypes by ensuring that each allele appeared in at least two or more independent PCRs and homozygous genotypes by ensuring that no more than one allele appeared in a total of four or more independent PCRs. Prior to inclusion in analyses of genetic relatedness, we used the software Cervus 3.0 (Kalinowski et al. 2007; Marshall et al. 1998) to calculate allele and genotype frequencies and observed and expected heterozygosity for each locus and to test each locus for deviation from Hardy-Weinberg equilibrium expectations and/or the presence of null alleles.

Resulting multilocus genotypes were then used to conduct likelihood-based parentage analyses and to derive partial pedigrees among animals in the study groups using Cervus 3.0 (Kalinowski et al. 2007; Marshall et al. 1998). We estimated the genetic relatedness between pairs of animals using the regression-based estimator of Queller and Goodnight (1989) and identified those pairs of individuals who were significantly more likely to be close kin (parent-offspring, full siblings, half siblings) than to be unrelated based on maximum likelihood ratios using the software KINGROUP 2 (Konovalov et al. 2004).

We compared the difference in average relatedness among same-sex adult dyads within social groups to see if group members of one sex were more closely related to one another, on average, than were members of the opposite sex. To determine if observed differences between dyad types were significant, we implemented a permutation test in which animal sex was randomly assigned (maintaining the same number of males and females as in the sampled focal group), and the average relatedness among simulated male-male and female-female dyads in the permuted dataset were calculated. At each permutation, we compared the calculated difference in average relatedness coefficients between simulated male-male and female-female dyads to the observed difference. We conducted 10,000 permutations for each focal social group and report *p*-values as the proportion of trials in which the observed difference was found to be less than the permuted difference.

Relationships between Social Structure and Genetic Relatedness

We evaluated the difference in SRI and PAI values between female-female, female-male, and male-male dyads each season using a resampling procedure with 10,000 iterations, followed by post-hoc pairwise permutation tests where appropriate. Permutation tests were implemented in R 3.3 (R, Core Team, 2014) using the ‘coin’ (Hothorn et al. 2008) and ‘rcompanion’ (Mangiafico 2017) packages.

The relationship between dyadic association patterns and genetic relatedness were investigated using the multiple regression quadratic assignment procedure (MRQAP) (Dekker et al. 2007; Krackhardt 1988) implemented in the software UCINET 6.6 (Borgatti et al. 2002). An extension of the Mantel (1967) test, MRQAP allows dependent matrices (i.e., the association matrix) to be regressed simultaneously against multiple independent matrices. For each field season, matrices of genetic relatedness were entered as independent variables, while the association matrix (either SRI or PAI) was entered as the dependent variable. To test if factors driving association differed by sex (e.g., whether males preferentially associated with kin while females did not), all MRQAP analyses were repeated using single-sex networks (i.e., networks constructed using only male and only female individuals). Following van Belle et al. (2014), we accounted for possible variation between study groups by creating a dichotomous matrix that assigned a value of 1 to all dyads from the same group and a value of 0 to all dyads between groups, then added the resulting matrix to each MRQAP analysis as an additional independent variable matrix.

RESULTS

Social Network Structure

Social networks created from SRI association indices, which are based on party composition data, revealed that all sampled individuals in the population could be connected, either directly or indirectly, into a single large network in both field seasons (Fig. 4.3). Edge weights in these two networks ranged from 0.008-0.89 among all dyads in 2014 and 0.001-0.99 among all dyads in 2015. The corresponding social network based on close proximity data collected in 2014 resulted initially in two separate components, one corresponding to individuals from social groups recognized *a priori* as C, D, and G, with individuals from group P forming a second, isolated component. In the close proximity network for 2015, no links were established between animals from the different putative social groups, resulting in four separate components that each corresponded to one of the groups recognized *a priori*. Edge weights among connected dyads within each component ranged from 0.002-0.132 in 2014 and 0.001-0.142 in 2015.

All constructed networks were found to have high maximum modularity scores (Q > 0.71), indicating strong and marked divisions between subsets of individuals within the population. These subsets clearly corresponded to the four focal social groups (C, D, G, and P) recognized *a priori* by researchers at the field site. Analyses aimed at detecting clustering within these social groups revealed clustering in some but not all networks based on party composition records (i.e., from SRI values) (Table 4.5). Clusters were more often identified in larger groups than smaller groups, likely due to their higher variation in association indices due to subgrouping behavior (Chapter 3; Ellis and Di Fiore in press). Nonetheless, all within-group networks constructed from SRI values had relatively low modularity scores (range of Q: 0.087-0.147), signifying that although clustering could be detected, it may not be indicative of true substructuring (i.e., individuals still associated quite frequently across potential clusters). Within-group social networks constructed from close proximity data (i.e., from PAI values), however, were more likely to return a Q value > 0.3, indicating that the associations among identified clusters were stronger than expected by chance, particularly at larger group sizes (Table 4.6). These high modularity scores for proximity based association networks suggest that even though party composition is not predictable, individuals may still prefer to interact, or simply tolerate, spatial proximity to particular others from their social group at finer spatial scales. Of the proximity based networks for each social group that had a modularity score Q > 0.3 (N = 9/16), identified clusters, or subunits (N = 29), were most often all female (27.6%) or comprised of multiple males and multiple females (27.6%), with only 17.2% of identified clusters either composed of one male and one female (10.3%) or a single male and multiple females (6.9%).

Hierarchical cluster analysis of SRI values using *modularity-G*, which breaks the bifurcating network into social units that maximize the difference in the strength of association indices within versus between social units, revealed four main clusters of animals in 2014 and five main clusters in 2015 (Fig. 4.4 a-d, upper panels). In 2014, these clusters corresponded to each of the four putative social groups, while in 2015, individuals recognized as being from social group P were themselves separated into two social units of five (2 SAMs, 1 AFD, 1 AF, 1 SF) and 10 (1 BAM, 2 SAMs, 5 AFDs, 2 AFs) individuals, respectively. However, when subadults were removed from analyses, this additional substructuring within social group P disappeared, and all adults were placed once again into one of four social units, each corresponding to one of the four putative social groups recognized *a priori*. Hierarchical cluster analysis of PAI values using *modularity-G* echoed this pattern, with all identified clusters matching those associated with groups C, D, G, and P (Fig. 4.5 a-d, upper panels). Mantel tests demonstrate that the strength of associations among individuals within identified clusters were significantly higher than those found for individuals between clusters (within cluster: 0.47±0.16 in 2014 and 0.47±0.15 in 2015; between: 0.01±0.1 in both 2014 and 2015; Table 4.7; Fig 4.6).

Complementary plots displaying the cumulative bifurcations of each cluster analysis showed different rates of change depending on the association index used (SRI versus PAI). Plots based on party composition data revealed a nearly constant rate of cumulative bifurcations with increasing association index value, compared to those based on close proximity data, which instead showed a logarithmic rate of increase (i.e., a high number of bifurcations at low association indices, before plateauing at higher association indices). In our 2015 dataset, we identified a significant change in the bifurcation rate (i.e., the slope above the "knot" was significantly different than the slope below the "knot") at an SRI value of 0.25 for the adult and subadult network and an SRI value of 0.3 for the adult only network. Using these inflection points as natural "cut-off" values for defining social units, all individuals fell into one of the four previously identified social groups, as we observed in the hierarchical cluster analyses using *modularity-G*. For the 2014 dataset, we found a significant change in the rate of cumulative bifurcations at an SRI value of 0.3 for the network including both adults and subadults, but no significant change was identified in the adult only network.

A more complicated picture emerges from the proximity-based association data, where the knots identifying the maximum rate of change in cumulative bifurcations do not immediately align with the four putative social groups, but rather occur within those social units (range of PAI cutoff values: 0.01-0.04; Fig. 4.5). Inspection of the bifurcating dendrograms reveal that these cutoffs reflect the variation in spatial proximity observed among members from the same social group, rather than between social groups, with a large number of individuals from the same social group found relatively infrequently within 5 m of one another (PAI < 0.05) and only a select few dyads, whom compared to their group members, are found within 5 m much more often (PAI > 0.05). Given that these identified knots, or cutoffs, are based on proximity scores rather than party composition scores, these plots likely reveal preferred relationships within each social group (e.g., "cliques") rather than distinct and hierarchically organized social tiers. Moreover, the strongest associations among networks comprised of both adults and subadults were among parents and their offspring (e.g., big adult male GIP and his subadult son GRY, and adult female COR and her subadult female CEL); however, once subadults were removed from the network, the strongest associations occurred among opposite sex pairs (e.g., adult male CLA and adult female CAL, adult male CRO and adult female GWN, and adult male DUK and adult female DAR). It should be noted that all three of the adult females previously listed were sexually receptive during the 2014 field season, successfully conceived, and gave birth during the summer of 2015.

Genetic Relatedness

All 12 microsatellite loci were found to be polymorphic, with the number of alleles per locus ranging between 4 and 19 (Table 4.4). We successfully genotyped 97.7% of loci across the dataset, with 71 of 86 (82.5%) individuals typed at all 12 loci and no individuals typed at fewer than 9 loci. The mean observed heterozygosity across the panel of loci was 0.770, and no locus deviated significantly from Hardy-Weinberg equilibrium genotype frequency expectations. The combination of loci used yielded a probability of identity (PI) value of 2.19×10^{-14} and a PI_{sib}

value of 1.22 x 10^{-5}, which means that, given allele frequencies in the population, there is an extremely low probability of any two individuals or any two full siblings, respectively, having identical multilocus genotypes by chance. In all, we genotyped 86 unique individuals, representing all age-sex classes.

Across all adults sampled in the population (N = 34 females, 20 males), we found no significant difference in the average relatedness within sexes (mean male R=-0.006±0.167 and mean female R = -0.006±0.156, P = 0.8732). Considering genotype data only for those adult individuals known to reside within the four social groups, the average estimated genetic relatedness among male-male dyads (N= 272 pairs, involving 17 males) and female-female dyads (N = 930 pairs, involving 31 females) was R = 0.026±0.161 and R = 0.004±0.156, respectively, while the average relatedness among male-female dyads (N=713) was R = -0.013±0.149. As within the overall population, we found no evidence that pairwise relatedness between male-male and female-female dyads within each group were significantly different than expected by chance (Table 4.8, Fig. 4.7).

Of the 52 adults and subadults included in social network analyses, 4.8% of dyads were identified through likelihood ratio tests as being more likely to be first order relatives (i.e., parent-offspring, full siblings, or half siblings) than to be unrelated. Adults of both sexes were commonly found to have adult first order relatives residing in both their own social group and in one or more neighboring groups (Fig 4.8). For example, FIN, a large adult male residing in group P during both field seasons, had one adult female first order (PHO) relative co-residing with him in that group and five additional inferred first order relatives residing in group G (four adult males [GOR, GDW, GIP, and GRY] and one adult female [GDV]). One adult female, OLV, did not have any inferred first-order relatives co-residing in her own group, but did have two close female relatives residing in neighboring group P (PTU and PEN).

Within groups, the proportion of adult males co-residing with close adult male kin was much higher than the proportion of adult females co-residing with adult female kin. In group C, two of three adult males were closely related while none of the dyads involving five sampled adult females were closely relatives. In group D, a similar pattern was found with four of five adult males being closely related, and zero of the adult females sharing high degrees of relatedness. For group G, two out of eleven adult females were found to be close kin, while three of the four adult males were closely related. Finally, in group P, we found that along with males (3/5), a high number of females (5/9) were co-residing with same-sex adult kin. However, given that two of the "adult" females sampled from group P were clearly young and seemingly nulliparous, the higher proportion of close female kin found in group P, at least compared to the other groups, may be the result of including pre-dispersed daughters among the set of adult females. When considering all groups together, adult males had a significantly higher number of close adult relatives of both sexes residing either in their own or in another focal group compared to adult females (males: 4±2.15, females: 2.46±1.14; Mann-Whitney Test: $U = 348$, $P = 0.011$).

Association Indices among Same-Sex and Inter-Sex Dyads and MRQAP

Permutation tests and pairwise comparisons found that association indices based on party membership (SRI values) were significantly higher among male-male dyads than among female-female dyads or male-female dyads in 2015 (Permutation Test: $P < 0.0026$; Fig. 4.9), meaning that during this period pairs of males were more likely to be found in the same subgroup than were other types of dyads. Closer inspection of SRI values among same-sex and between-sex dyads, partitioned by group, suggest that these patterns were most likely driven by the males in the two larger social groups, groups G and P (Fig. 4.10). For association indices based on proximity data (PAI values), no particular dyad type was found to spend significantly more time in close proximity than any other (Permutation Test: 2014, $P = 0.292$; 2015, $P = 0.118$).

In MRQAP analyses, SRI values were significantly and positively correlated with estimated genetic relatedness for 2014, but not 2015 (Table 4.9). We found no correlation between relatedness and the percent of time pairs of animals spent in the same subgroup for either the female-only or male-only networks, suggesting that the positive correlation found in 2014 may have been driven by a tendency for related individuals of different sex to be found together in the same subgroups. By contrast, PAI values among the entire set of sampled animals were significantly and positively correlated with inferred genetic relatedness for both the 2014 and 2015 field seasons. When considering the female-only and male-only networks, we found that closely related females were more likely to spend time within 5 m of each other compared to non-related females in both time periods, and males were more likely to be in close proximity to male kin in 2015, though not in 2014. However, we noted, *post hoc*, that based on parentage analyses and likelihood estimates of full and half sibling relationships, these positive correlations were most likely driven by the tendency of subadult females to maintain close association with their mothers and of subadult males to maintain close association with their fathers and their adult full- and half-brothers. We thus re-ran the female-only and male-only MQRAP analyses using only adult individuals and found that, indeed, close relatives of the same sex were no more likely than non-relatives of the same sex to be found in spatial proximity.

DISCUSSION

Our study is one of the first to combine observational and molecular data with social network analysis to better understand the factors influencing woolly monkey grouping dynamics. Association patterns among woolly monkeys sampled in two four-month periods at the Tiputini Biodiversity Station yielded one large network comprising four distinct clusters, each of which corresponded to our *a priori* classifications of social groups (C, D, G, and P). Although individuals preferentially associated with members of a single social group, associations with animals from outside of that social group were not uncommon, particularly between members of social groups C and G, which have home ranges that overlap extensively (see Chapter 3; Ellis and Di Fiore in press). Additionally, we found no evidence of a difference in the average relatedness of male-male and female-female dyads, either within social groups or across the entire set of individuals sampled from four neighboring groups, which suggests a lack of strongly sex-biased dispersal. Still, across our study population males had, on average, a greater number of close same-sex kin than females did, a pattern also seen in another local population of woolly monkeys from the same region (Di Fiore and Fleischer 2005). Moreover, animals of both sexes had ample opportunities to interact with close kin, as both males and females often had genetic relatives residing either within their social group, in a neighboring social group, or, more commonly, both. Indeed, we found that close proximity associations (< 5 m) among females were significantly correlated with genetic relatedness in both 2014 and 2015, and proximity association indices among males were significantly correlated with genetic relatedness in 2015. However, these patterns were not driven by associations between adult kin, but rather by the strong spatial associations between parents and their subadult offspring.

For animals exhibiting fission-fusion dynamics, delineating what and who constitutes a group can be difficult (Sundaresan et al. 2007; Whitehead 2008). Yet, determining the variation in non-random associations among individuals in a population is important for understanding both how social structure may impact an individual's behavior and fitness and how network topology can influence the ability for individuals to cooperate, communicate, and exchange information or pathogens (Krause et al. 2007; Sih et al. 2009; Wey et al. 2008). In this study, we used metrics of network modularity and hierarchical clustering analysis to identify the underlying structure of woolly monkey society. Using both methods, we found that, regardless of season or type of association (SRI and PAI) used to derive the network, the individual woolly monkeys sampled during our study were consistently and robustly divided into one of four clusters that corresponded to social groups recognized *a priori* by researchers at the site. The overall network structure was found to be highly modular, with individuals associating more often with others from the same cluster (or social group), rather than between clusters. Taken together, these analyses provide support that our field identifications and *a priori* assessment of distinct social groups likely represent true divisions of the population, and that these divisions are likely to be meaningful to the animals themselves.

Though the woolly monkeys sampled in this study were unequivocally divided into four distinct social units, we found little direct evidence of consistent substructure below the level of the social group using modularity. For example, clusters based on party composition could be identified in some, but not all, within-group social networks, and when identified, the modularity scores for these networks were very low ($Q < 0.3$). The lack of confident subdivisions within social groups demonstrates that although groups may regularly fission into separate subgroups (especially at larger group sizes), these subgroups do not necessarily consist of the same sets of individuals. When investigating proximity-based association patterns within each social group, individuals were more confidently divided into different subunits, particularly as group size increased. This pattern suggests that some individuals may either seek out and associate in close proximity with a particular set of other individuals from their social group, or simply tolerate spatial proximity to these individuals more so than others.

In contrast to a majority of multi-tiered primate societies, in which the most basal social unit is comprised of a single “leader” male and one or more females (e.g., geladas [Dunbar and Dunbar 1975; Kawai et al. 1983; Snyder-Mackler et al. 2012], hamadryas baboons [Kummer 1968; Schreier and Swedell 2009; Swedell 2006], guinea baboons [(Galat-Luong et al. 2006; Patzelt et al. 2014; Sharman 1982], snub-nosed monkeys], and proboscis monkeys [Yeager 1990], only 17.2% of the clusters confidently identified through modularity were composed of a single male and one or more females. Instead, most clusters based on spatial proximity were either sex-segregated (all female clusters) or comprised of multiple males and multiple females. The prevalence of all female subunits may reflect a difference in nutritional requirements between males and females, particularly for those females that are either gestating or lactating. In fact, the preference for lactating females to associate or form subgroups with other lactating females is not uncommon in large-bodied frugivorous primates with fission-fusion dynamics (e.g., chimpanzees [Sakura 1994], spider monkeys [Chapman 1990; Slater et al. 2009], and orangutans [van Schaik 1999]), and the formation of such subunits may offer increased opportunities for infant socialization and/or reduced feeding competition.

Hierarchical cluster analysis using proximity-based associations for the whole network (not just within group) corroborated the concept of individuals having preferred association partners within their social groups given that the association indices found to differentiate between social tiers based on bifurcation plots were located within rather than between identified social groups. These results were most likely driven by the low association indices of most group mates at close spatial proximity, with relatively few dyads regularly associating within 5 m of one another. Among adults, the highest association rates were most often found among opposite sex pairs. During the 2014 field season, when mating was more common, these dyads frequently comprised an adult male and a sexually receptive female. In 2015, these same females continued to maintain higher degrees of spatial proximity to particular males, even after parturition. Although no significant differences were found among proximity-based association indices of same-sex or opposite sex dyads using permutation tests, the select male-female relationships observed in hierarchical cluster analysis highlight an intriguing difference in preferred association partners between woolly monkeys and their closest relatives, spider monkeys and muriquis, who more commonly associate with individuals of the same sex rather than those of the opposite sex (Ramos-Fernández et al. 2009; Strier 1997; Strier et al. 2002; Symington 1987). Both Nishmura (1994) and Di Fiore and Fleischer (2005) have previously shown that among non-juvenile woolly monkeys male-female associations occur more often than expected by chance, while associations among same-sex individuals are relatively rare, at least at very close spatial scales (< 1 m). Given that females actively solicit males for mating opportunities and tend to be the ones that initiate grooming bouts, Di Fiore and Fleischer (2005) have suggested that some females may find benefits in developing and fostering “friendships” with particular males. Such benefits may include increased fitness for the female, and if present, her offspring, by offering male protection against threats of male infanticide, female harassment, and predators, or simply by tolerating the female’s proximity in feeding contexts and actively sharing food resources (Baniel et al. 2016; Moscovice et al. 2009, 2010; Palombit et al. 1997). However, by seeking out and maintaining spatial proximity to particular females, males may also accrue benefits, such as increasing paternity certainty with a receptive female. Moreover, in cases where females currently have a young dependent, males may display greater interest in both the female and her infant to a) provide direct paternal care to his (potentially) sired offspring or to b) improve his chances of mating with that female in the future (Kerhoas et al. 2016; Langergraber et al. 2013; Ménard et al. 2001; Ostner et al. 2013; Palombit et al. 1997; Smuts 1985).

Although we found no significant differences in average relatedness among adult female-female, female-male, or male-male dyads either across the sampled population or within the four focal social groups, adult males had nearly twice as many close adult kin residing in the population as adult females did. Despite having close kin available, we found no evidence among adults that genetic relatives associated with one another (either in the same party or in close spatial proximity) significantly more often than non-genetic relatives. Provided that male-male dyads, at least in 2015, had significantly higher association indices compared to female-female or female-male dyads based on party composition data, males may still find benefits to associating at least at the party level with other males, even if unrelated. For example, males may receive mutual benefits by cooperatively defending food resources or receptive females from other social groups or extragroup males. In fact, male cooperation in woolly monkeys is most readily apparent during aggressive intergroup encounters, where males from the same social group band may together in coordinated effort to displace other males (and sometimes females) through chases and physical attacks (Di Fiore 1997; Di Fiore et al. 2011; Ellis, personal observation). Alternatively, the significantly higher prevalence of male-male associations at the party level may not be the result of males seeking out other males, but rather a residual product of males simultaneously monitoring the same receptive females in their social group. Given that mating is promiscuous and occurs in the open, and that males are highly tolerant of one another (Di Fiore and Fleischer 2005), this explanation seems equally plausible.

Overall, our genetic results strongly suggest that dispersal from the natal group is not limited to females, as is reported to be the case in other atelin primates (spider monkeys and muriquis), and likewise imply that a substantial number of males also disperse from their natal groups. Dispersal by both sexes was previously reported by Di Fiore and colleagues (2009) when evaluating dispersal patterns among spider monkeys and woolly monkeys in the Yasuní region 10+ years ago, indicating that this is likely a pattern for the population as a whole and not just a product of the individuals sampled during this study. The reason why some males disperse while others remain in their natal groups is not known, but it may have to do with limited reproductive opportunities within their natal social unit. For example, in one study of muriquis (*Brachyteles*, the sister genus to *Lagothrix*), two males were observed to leave their natal group at 5 and 8 years of age, and both attempted to immigrate into a smaller group with a more favorable sex ratio (Cavalcante et al. 2016). Only the younger male was successful, while the older male returned to his natal group. Similar patterns of exploration and dispersal have been observed at TBS involving two collared males thought to be natal to our two smallest focal groups (C and D). Gael (GAE) was captured and collared in 2012 as a small adult male. When originally captured he was believed to be a member of group C, the group in which his mother, Gwen (GWN), currently resides. Focal follows of Gael throughout the summer of 2012 often found him ranging alone within Group C's small home range, but his ranging also extended to some degree into the home range of group G (beyond the overlap area normally shared between the two groups). By the summer of 2013, Gael was occasionally seen interacting with members of group C, but he was most often observed ranging either alone within the home range of group G or with members of group G in mixed-sex parties. By 2014, Gael was fully integrated into group G and observed mating with several of the adult females in that group. The second male was first observed in 2014 as an older subadult male transitioning into a small adult male and associating with members of group D. This male was seen regularly in the first two months of study, but he would often leave the group for extended periods of time. In 2015, this male was only spotted twice interacting with members of group D. Finally, in 2017, this male was captured and collared in a neighboring group (Group I), where he remains to this day.

Finally, our molecular results confirm previous findings that adult woolly monkeys have a dispersed network of same- and opposite-sexed kin residing within and between adjacent social groups (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). In western lowland gorillas, the presence of a dispersed network of kin, particularly among closely related silverback males, is thought to facilitate peaceful and tolerant intergroup encounters (Bradley et al. 2004). Among woolly monkeys, tolerant intergroup encounters have long been noted to occur, with individuals from two or more social groups found periodically resting, traveling, and/or foraging together in close spatial proximity for extended periods of time (e.g. hours) and without overt aggression (Defler 1996; Di Fiore 1997; Di Fiore et al. 2009; Nishimura 1990; Peres 1994). In fact, of the 102 intergroup encounters observed during our 2014 and 2015 field seasons (see chapter 3; Ellis and Di Fiore in press), nearly 60% were deemed “tolerant”, meaning that individuals from different social groups were either engaged in affiliative behavior such as grooming or mating or displaying more neutral behaviors such as co-feeding or traveling within 10 m of one another without conflict. Given that males are often the individuals most conspicuously and overtly involved in agonistic intergroup encounters, a male’s recognition of kin outside of his own social group – and perhaps particularly male kin – may play a crucial role in neutralizing rising tensions during intergroup encounters and permit for more peaceful and amicable interactions. Still, we must also acknowledge the prospect that dispersed males (and females) may not be relying solely on kin recognition, per se, when making decisions about how to interact with individuals from other groups during intergroup encounters, but rather on their social familiarity with others from their natal group, such as age-mates, who they may or may not be genetically related to. We look forward to exploring more explicitly how this dispersed network of kin may impact intergroup relations in our future work.

TABLES

Table 4.1. Definition of terms used to describe social structure throughout this chapter.

Term	Definition	Citation
Cluster	A set of individuals that repeatedly associate together such that they form a distinct social unit which is revealed through an objective analytical clustering method.	de Silva et al. 2011
Component	A component is a connected network where there is a path between every pair of nodes (i.e., all nodes are reachable). In some cases, networks may be disconnected and partitioned in to different subsets. When there are paths connecting nodes within a subset, but no paths between nodes in different subsets, these networks are considered separate components.	Wasserman and Faust 1994
Gambit of the Group	Method for accumulating relational data and is based on the assumption that when conspecifics are clustered together in space and/or time they are interacting with one another.	Whitehead and Dufault 1999
Multilevel Society	Any society in which an individual differentially associates with more than one set of companions. Unlike multitiered societies, social units in a multilevel society are not always nested or hierarchical.	de Silva and Wittemyer 2012
Multitiered Society	A society in which an individual differentially associates with more than one set of companions, and social affiliations among individuals are stratified into different, hierarchical levels, called social tiers.	
Network	A network consists of a set of individuals and the relations defined on them. Relations, in this sense, refer to the collection of ties of a given kind measured on each pair of individuals. Here, the strength of ties between individuals were calculated using association data collected at two spatial scales, party membership and close spatial proximity (<5 m).	Wasserman and Faust 1994

Table 4.1. continued

Party	A set of conspecific animals that are observed in spatiotemporal proximity with one another and often engaged in coordinated activities such as moving, resting, feeding, and socializing. Here, animals were considered to be in the same party when they maintained visual or low intensity vocal contact with one another 15 minutes before, during, or after each sampling period and were located at a distance of no more than 100 m from at least one other party member following a chain. Parties could consist of all the individuals or a subset of the individuals from a single social group as well as all of the individuals or a subset of the individuals from two or more social groups.	
Social Group	Sets of conspecific animals that are permanently or nearly permanently in association, that actively maintain spatiotemporal proximity with one another across time, and are often observed moving, resting, feeding, and interacting non-aggressively.	
Social Structure	The spatiotemporal patterning of social associations among conspecifics.	Hinde 1976; Kappeler and van Schaik 2002
Social Unit	Set of conspecific animals that are socially affiliated, interact regularly, and do so more with each other than with members of other such units.	Kappeler and van Schaik 2002; Struhsaker 1969
Subgroup	A subset of conspecifics that belong to the same social group that are actively maintaining spatiotemporal proximity to one another and demonstrating coordinated activity. Subgroups are differentiated from parties (defined above) in that the latter may consist of individuals from different social groups while the former consists only of individuals from the same social group.	

Table 4.2. Composition of the four putative woolly monkey social groups recognized a priori between August 2014 and December 2015 at the Tiputini Biodiversity Station, Ecuador.

	Group C		Group D		Group G		Group P	
Age-Sex	2014	2015	2014	2015	2014	2015	2014	2015
Adult Male	2	3	5	4	3	4	4	4
Subadult Male	1	-	1	-	2	2	-	1-2
Adult Female	5	4-5	6	5-6	10-11	8-9	9	10
Subadult Female	1	1	-	-	4	3-4	2	2
Juvenile	5	4	5	5	6	7	7	7
Infant	-	1-2	2	1	4	2	2	3
Adults and Subadults	9	8-9	12	9-10	19-20	17-19	15	17-18
Total with Dependents	14	13-15	19	15-16	29-30	26-28	24	27-28

Table 4.3. Summary of focal data collected on animals belonging to four putative social groups of woolly monkeys at the Tiputini Biodiversity Station, Ecuador. Data are separated by field season (2014 and 2015) and include individual identities, putative group membership, number of hours of observational data collected, and whether or not a genetic sample was obtained. Note the disproportionate number of observation hours on individual Gwen from social group C in 2015.

Focal Animal	Three Letter Code	Group	2014 Age/Sex	2014 Total (hrs)	2015 Age/Sex	2015 Total (hrs)	Grand Total (hrs)	Genetic Sample
Café	CAF	C	-	-	AF	15.00	15.00	N
Cali	CAL	C	AF	9.75	AFD	29.83	39.58	Y
Celeste	CEL	C	SF	21.75	SF	30.92	52.67	Y
Chai	CHA	C	AFD	31.50	AF	45.45	76.95	Y
Chloe	CHL	C	JF3	8.67	SF	3.83	12.50	Y
Clash	CLA	C	SAM	39.92	SAM	31.17	71.08	Y
Coco	COC	C	AFD	34.33	-	-	34.33	Y
Cora	COR	C	AF	33.50	AF	70.10	103.60	Y
Chrome	CRO	C	BAM	45.58	BAM	31.75	77.33	Y
Cuzco	CUZ	C	SM	35.08	SAM	31.67	66.75	Y
Gwen	GWN	C	AF	41.42	AFD	204.30	245.72	Y
Dahlia	DAH	D	AFD	4.83	AFD	24.83	29.67	N
Daeo	DAO	D	SAM	2.67	SAM	24.00	26.67	Y
Darlene	DAR	D	AF	9.75	AFD	32.17	41.92	Y
Dash	DAS	D	SM	26.63	SAM	33.00	59.63	Y
Delta	DEL	D	AFD	10.38	-	-	10.38	Y
Digit	DIG	D	AM	34.17	-	-	34.17	Y
Diya	DIY	D	AFD	23.83	AFD	18.58	42.42	Y
Delilah	DLL	D	AFD	25.25	AFD	27.83	53.08	Y
Docket	DOC	D	AM	27.42	AM	36.42	63.83	Y
Daisy	DSY	D	-	-	AF	11.25	11.25	Y
Duke	DUK	D	SAM	17.42	SAM	29.08	46.50	Y
Olivia	OLV	D	AFD	28.92	AF	26.02	54.93	Y
Calliope	CLP	G	AF	8.92	AF	23.50	32.42	Y
Gabby	GAB	G	SF	8.42	SF	28.17	36.58	Y
Gael	GAE	G	AM	26.08	AM	29.50	55.58	Y
Gala	GAL	G	AFD	21.50	AFD	22.08	43.58	Y
Godiva	GDV	G	AFD	30.42	AFD	23.08	53.50	Y
Goodwin	GDW	G	AM	11.83	AM	22.83	34.67	Y
Geena	GEE	G	AF	4.00	-	-	4.00	N

Table 4.3 continued

Gillian	GIL	G	AFD	25.58	AF	17.00	42.58	Y
Gin	GIN	G	JM3	0.00	JM3	0.92	0.92	Y
Gipmunk	GIP		BAM	39.53	BAM	29.50	69.03	Y
Gisella	GIS	G	AFD	4.00	AFD	34.33	38.33	Y
Gita	GIT	G	AFD	19.50	AF	17.50	37.00	Y
Grammy	GMA	G	AF	5.58	-	-	5.58	N
Gemima	GMM	G	AFD	5.58	AFD	25.58	31.17	Y
Ginger	GNG	G	SF	0.00	SF	33.67	33.67	Y
Ginny	GNY	G	AF	7.25	-	-	7.25	N
Gordon	GOR	G	SM	28.08	SAM	34.67	62.75	Y
Greta	GRE	G	AF	8.33	AF	27.08	35.42	Y
Gertie	GRT	G	SF	8.25	SF	9.67	17.92	N
Grayson	GRY	G	SM	12.92	SM	35.83	48.75	Y
Gus	GUS	G	JM3	0.00	JM3	1.17	1.17	Y
Finn	FIN	P	BAM	26.08	BAM	20.92	47.00	Y
Paddy	PAD	P	AM	24.08	AM	15.52	39.60	Y
Paleta	PAL	P	AF	3.58	AFD	19.08	22.67	Y
Penelope	PEN	P	AFD	6.25	AF	20.42	26.67	Y
Pete	PET	P	SAM	25.33	SAM	15.83	41.17	Y
Phoebe	PHO	P	AF	10.42	AF	16.25	26.67	Y
Phyllis	PHY	P	AF	2.17	AFD	23.42	25.58	Y
Piper	PIP	P	AFD	23.83	AFD	37.00	60.83	Y
Paloma	PLM	P	SF	0.00	SF	7.75	7.75	N
Podrick	POD	P	-	-	SM	11.17	11.17	Y
Portia	POR	P	-	-	AFD	19.75	19.75	N
Percy	PRC	P	AM	43.75	AM	40.58	84.33	Y
Pearl	PRL	P	AFD	12.58	AFD	23.92	36.50	Y
Prudence	PRU	P	SF	7.83	-	-	7.83	N
Patsy	PTC	P	AF	3.00	AF	12.33	15.33	Y
Petunia	PTU	P	AF	11.25	AFD	16.00	27.25	Y
Purdue	PUR	P	JM3	4.58	JM3	0.00	4.58	Y
Pyf	PYF	P	-	-	AF	9.33	9.33	Y
Grand Total				993.3		1482.55	2475.85	

Female Categories: AF-Adult Female without Dependents (<2 years of age), AFD - Adult Female with Dependent (<2 years of age), SF -Subadult Female, JF3-Large Juvenile Female
Male Categories: BAM - Big Adult Male, SAM- Small Adult Male, SM - Subadult Male, JM3-Large Juvenile Male

Table 4.4. Genetic variability of 12 microsatellite loci used to genotype 86 woolly monkeys from the Tiputini Biodiversity Station, Ecuador.

Locus	N	N_a	H_o	H_e	Significance	Reference
AB 06	81	9	0.815	0.837	NS	1
Apm01	83	10	0.867	0.815	NS	2
D17S804	82	12	0.829	0.838	NS	3
Leon 2	84	7	0.405	0.443	NS	4
Leon 21	82	7	0.768	0.744	NS	4
LL 1-1#10	83	10	0.819	0.857	NS	5
LL 1-1#15	86	9	0.872	0.814	NS	5
LL 1-1#18	86	12	0.872	0.859	NS	5
LL 1-1#3	85	19	0.953	0.927	NS	5
LL 1-5#7	86	5	0.756	0.725	NS	5
LL 3-1#2	86	4	0.535	0.542	NS	5
Locus 5	84	6	0.750	0.722	NS	6
Average		9.167	0.770	0.760		

N = number of individuals genotyped; N_a = number of alleles; H_o = observed heterozygosity; H_e = expected heterozygosity under Hardy-Weinberg equilibrium; NS = not significant with Bonferroni correction ($p > 0.05$).

[1]Goncalves et al. 2004; [2]Cortes-Ortiz et al 2010; [3]Weissenbach et al. 1992; [4]Perez-Sweeny et al. 2005; [5]Di Fiore and Fleischer 2004; [6]Grativol et al. 2001.

Table 4.5. Modularity scores (Q), the number of clusters detected, and the composition of those clusters based on the simple ratio indices (SRI) calculated for four identified groups of woolly monkeys in two field seasons (2014 and 2015). Results include two different networks, one with adults and subadults together and one with adults only. Note, that although clusters could be identified in some within group networks, modularity scores were <0.3 in all cases, indicating that these social units are less likely to represent true subdivisions within the social group.

Group		SRI-2014 All	SRI-2014 Adults Only	SRI-2015 All	SRI-2015 Adults Only
C	Modularity (Q)	0.114	0.147	0.112	0.126
	No. of Clusters	1	1	1	1
	Composition of Clusters				
D	Modularity (Q)	0.098	0.103	0.101	0.101
	No. of Clusters	2	2	1	1
	Composition of Clusters	1: 1 AF, 4 AFDs	1: 1 AF, 4 AFDs		
		2: 2 AMs, 2 SAMs, 1 SM	2: 2 AMs, 2 SAMs		
G	Modularity (Q)	0.099	0.092	0.106	0.102
	No. of Clusters	3	2	3	3
	Composition of Clusters	1: 2 AF, 4 AFDs, 1 SF	1: 2 AFs, 3 AFDs	1: 1 AF, 2 AFDs, 1 SAM, 1 SF	1: 1 AF, 2 AM, 1 BAM
		2: 2 SFs	2: 1 AF, 3 AFDs, 1 BAM, 2 SAMs	2: 1 AF, 2 AM, 1 BAM, 1 SM	2: 3 AFs, 2 AFDs
		3: 1 AF, 2 AFDs, 1 BAM, 2 SAMs,		3: 2 AF	3: 2 AFDs, 1 SAM
P	Modularity (Q)	0.089	0.087	0.140	0.128
	No. of Clusters	2	1	3	3
	Composition of Clusters	1: 4 AF, 2 AFDs, 2 AMs, 1 SAM		1: 1 AF, 3 AFDs, 1 AM, 1 BAM	1: 1AF, 3 AFDs, 1 AM, 1 BAM
		2: 1 AF, 1 AFD, 1 BAM, 2 SFs		2: 2 AFDs	2: 1 AF, 1 AFD, 1 SAM, 1 SM
				3: 2 AF, 1 AFD, 1 AM, 1 SAM, 1 SF, 1 SM	3: 1 AF, 2 AFDs, 1 AM

Table 4.6. Modularity scores (Q), the number of clusters detected, and the composition of those clusters based on association indices of spatial proximity (<5 m) calculated for four identified groups of woolly monkeys in two field seasons (2014 and 2015). Results include two different networks, one with adults and subadults together and one with adults only. Note, that although clusters could be identified in all within group networks, only some of these networks (highlighted in bold) have modularity scores > 0.3, indicating a more confident assessment of subdivisions within the social group at this close spatial scale.

Group		PAI-2014 All	PAI-2014 Adults Only	PAI-2015 All	PAI-2015 Adults Only
C	Modularity (Q)	0.219	0.243	**0.326**	0.195
	No. of Clusters	3	2	**3**	3
	Composition of Clusters	1: 1 AF, 1 AFD, 1 SF	1: 1 AF, 1 SAM	**1: 1 AF, 1 SF, 1 SM**	1: 1 AF, 1 BAM
		2: 1 AF, 1 SAM, 1 SM	2: 2 AF, 2 AFDs, 1 BAM	**2: 2 AF, 1 AFD, 1 BAM, 1 SAM**	2: 1 AF, 1 AFD, 1 SAM
		3: 1 AF, 1 AFD, 1 BAM			3: 1 AF, 1 SAM
D	Modularity (Q)	**0.303**	**0.350**	0.199	0.199
	No. of Clusters	**3**	**3**	3	3
	Composition of Clusters	**1: 1 AF, 1 SAM**	**1: 1 AF, 1 SAM**	1: 1 AF, 2 AFDs, 1 AM	1: 1 AF, 2 AFDs, 1 AM
		2: 2 AMs, 1 SM	**2: 2 AMs**	2: 2 AFDs, 2 SAMs	2: 2 AFDs, 2 SAMs
		3: 3 AFDs	**3: 3 AFDs**	3: 1 AF, 1 SAM	3: 1 AF, 1 SAM
G	Modularity (Q)	**0.327**	0.218	**0.420**	0.288
	No. of Clusters	**3**	3	**4**	3
	Composition of Clusters	**1: 1 AF, 3 AFDs, 1 SF, 2 SAMs**	1: 2 AFDs, 1 BAM, 1 SAM	**1: 2 AFs, 1 AM, 1 BAM, 1 SM**	1: 1 AF, 3 AFDs, 1 AM
		2: 1 BAM, 1 SM, 1 SF	2: 1 AFD, 1 SAM	**2: 1 AFD, 1 SF**	2: 1 AF, 2 AFDs, 1 AM, 1 SAM
		3: 1 AFD, 1 SM	3: 1 AF, 1 AFD	**3: 1 AF, 1 AFD, 1 AM, 1 SAM, 1**	3: 1 AFD, 1 BAM
				4: 1 AF, 2 AFDs	
P	Modularity (Q)	**0.307**	**0.332**	**0.403**	**0.381**
	No. of Clusters	**4**	**3**	**3**	**2**
	Composition of Clusters	**1: 1 AF, 1 AFD**	**1: 1 AF, 1 AM, 2 SAMs**	**1: 2 AFDs, 1 AM, 1 SF**	**1: 1 AF, 3 AFDs, 1 AM, 1 SAM**
		2: 1 AFD, 1 BAM	**2: 1 AF, 1 AFD, 1 BAM**	**2: 2 AFs, 3 AFDs, 1 BAM, 1 AM**	**2: 2 AF, 3 AFDs, 1 AM, 1 BAM**
		3: 1 AF, 2 AMs, 1 SAM	**3: 1 AF, 1 AFD**	**3: 1 AFD, 1 SAM, 1 SM**	
		4: 1 AF, 1 SF			

Table 4.7. Mantel Tests comparing association indices (SRI and PAI) within clusters versus between clusters from 2014 and 2015. Clusters were identified by hierarchical cluster analysis using the average linkage method and were found to correspond to each of the four focal social groups (C, D, G, and P). Tests were conducted both on matrices containing all focal individuals (adults and subadults) as well as adults only.

		Within Clusters mean AI ± SD	Between Clusters mean AI ± SD	t	p	CCC	Max Modularity	AI Cutoff
SRI	2014 Adults and Subadults	0.47 ± 0.16	0.01 ± 0.01	30.526	<0.001	0.983	0.719	0.175
	2014 Adults Only	0.48 ± 0.14	0.01 ± 0.01	25.216	<0.001	0.989	0.711	0.156
	2015 Adults and Subadults	0.47 ± 0.15	0.01 ± 0.01	31.896	<0.001	0.983	0.719	0.278
	2015 Adults Only	0.48 ± 0.13	0.01 ± 0.00	27.456	<0.001	0.983	0.725	0.295
PAI	2014 Adults and Subadults	NA	NA	NA	NA	0.900	0.726	0.003
	2014 Adults Only	NA	NA	NA	NA	0.905	0.734	0.004
	2015 Adults and Subadults	NA	NA	NA	NA	0.922	0.775	0.0002
	2015 Adults Only	NA	NA	NA	NA	0.896	0.748	0.0001

Table 4.8. Average estimated pairwise relatedness among dyads of adult females and dyads of adult males in four putative social groups of woolly monkeys at the Tiputini Biodiversity Station, Ecuador.

Group	Mean Female Relatedness (mean ± sd)	# Adult Females	Mean Male Relatedness (mean ± sd)	# Adult Males	Absolute Difference between means for each sex	*p*-value
C	-0.019 ± 0.065	5	-0.026 ± 0.096	3	0.007	0.939
D	-0.057 ± 0.116	5	0.043 ± 0.175	5	0.100	0.077
G	-0.030 ± 0.154	11	0.050 ± 0.176	6	0.079	0.113
P	-0.059 ± 0.138	9	-0.018 ± 0.138	4	0.077	0.225

p-value calculated based on permutation tests with 10,000 permutations for each group.

Table 4.9. Results from MRQAP analyses assessing the relationship between woolly monkey spatial associations and genetic relatedness in a 1) complete network consisting of all adults and subadults of both sexes, 2) a female-only network, and 3) a male-only network, calculated for both the 2014 and 2015 study periods. Analyses were then repeated for adult-only versions of the complete, female-only, and male-only networks.

Association Index - Year	Total Network		Female Network		Male Network	
	Correlation Coefficent	*p*	Correlation Coefficent	*p*	Correlation Coefficent	*p*
SRI - 2014						
Relatedness Adults and Subadults	**0.036**	**0.016**	0.034	0.246	0.013	0.389
Relatedness Adults Only	-0.009	0.596	-0.015	0.585	-0.008	0.697
(N = 27 AF, 13 AM, 6 SF, 4 SM)						
SRI - 2015						
Relatedness Adults and Subadults	**0.045**	**0.001***	0.047	0.066	0.029	0.385
Relatedness Adults Only	0.018	0.269	-0.011	0.735	0.022	0.474
(N = 27 AF, 16 AM, 5 SF, 2 SM)						
PAI - 2014						
Relatedness Adults and Subadults	**0.121**	**0.002***	**0.199**	**0.012**	0.155	0.059
Relatedness Adults Only	0.058	0.096	0.045	0.347	0.142	0.173
(N = 19 AF, 12 AM, 5 SF, 3 SM)						
PAI - 2015						
Relatedness Adults and Subadults	**0.088**	**0.009***	**0.179**	**0.005***	**0.205**	**0.024**
Relatedness Aduts only	-0.010	0.422	0.074	0.056	0.132	0.084
(N = 27 AF, 16 AM, 5 SF, 1 SM)						

AF = adult female, AM = adult male, SF = subadult female, SM = subadult male.

Bold values are significant to $p < 0.05$; * indicates that values are significant after Bonferroni correction for multiple tests.

FIGURES

Figure 4.1. Location of the Tiputini Biodiversity Station and the observed home ranges (95% kernel density estimates) of eight woolly monkey groups that range throughout the study area (modified from Di Fiore et al. 2009).

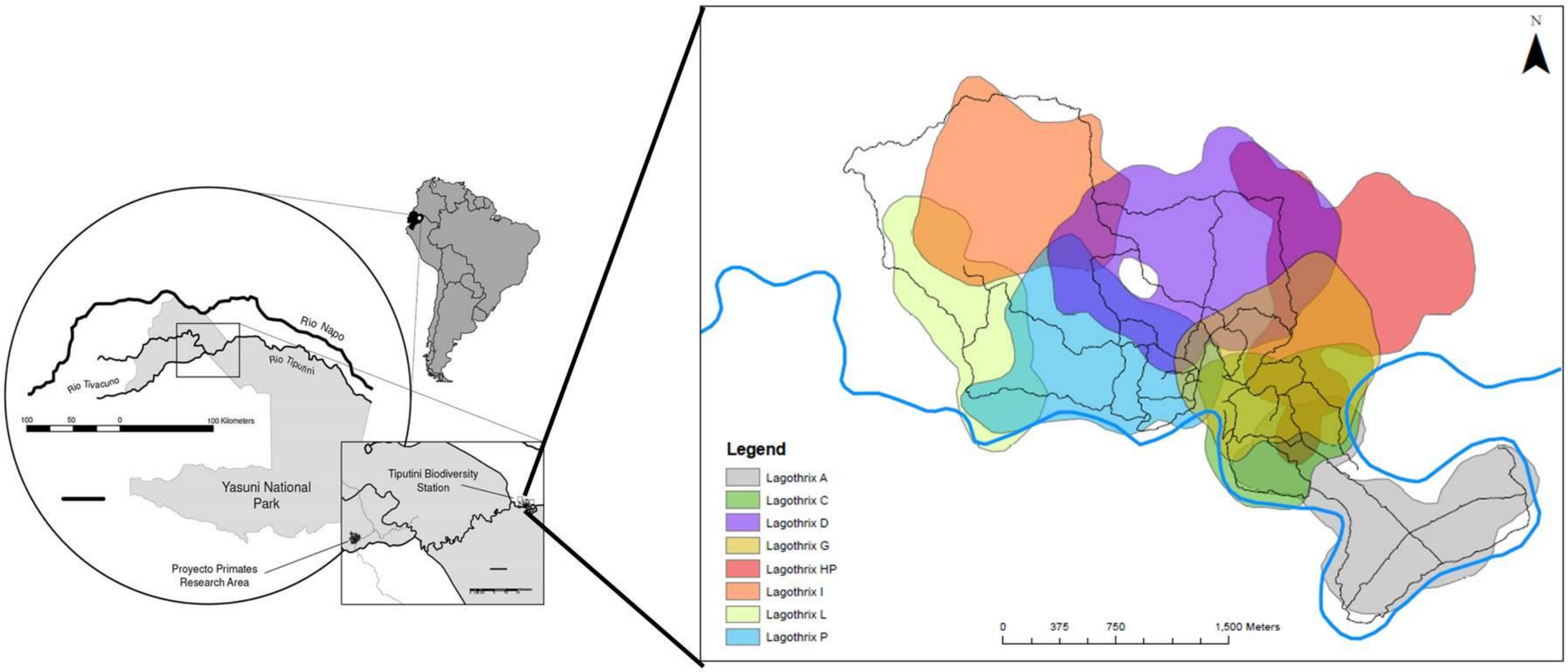


Figure 4.2. “Survival” curve of distances between two simultaneously followed individuals from the same social group used to corroborate distance thresholds for classifying animals as being part of the same or different subgroups. To determine when association patterns were most likely qualitatively and quantitatively different from close spatial associations we fit two linear regressions to subsets of the data following 10 m increments until we found the two subsets that had the lowest combined sum of squares of the residuals (e.g., for a group with a maximum interindividual distance of 1000 m we fit linear regressions to 0-10 m and 10-1000 m, calculated the sum of squares of the residuals between each regression line, then fit regressions to 0-20 m and 20-1000 m, and so on. After all combinations were reached, we then identified the combination that created the lowest sum of squares of the residuals). The intersection of these two best fit regression lines ranged from 80-130 m, depending on group size.

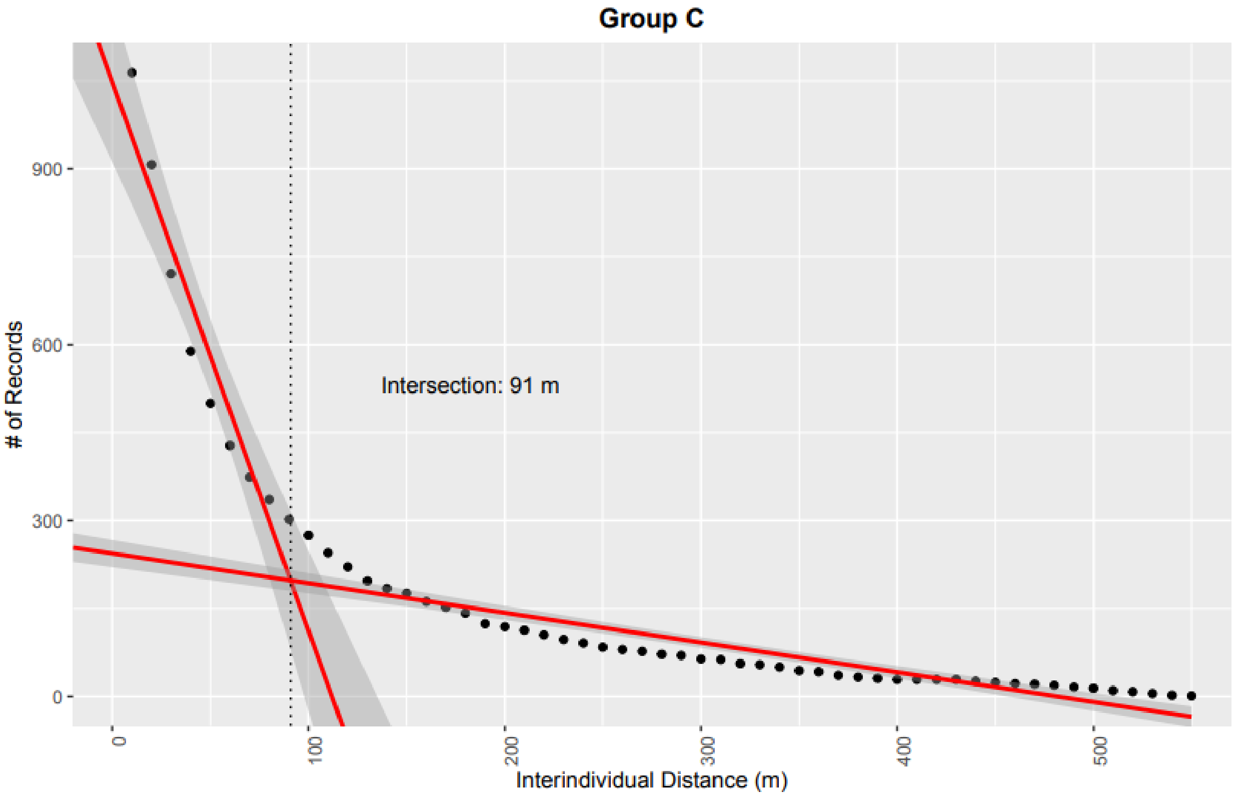


Figure 4.2 continued.

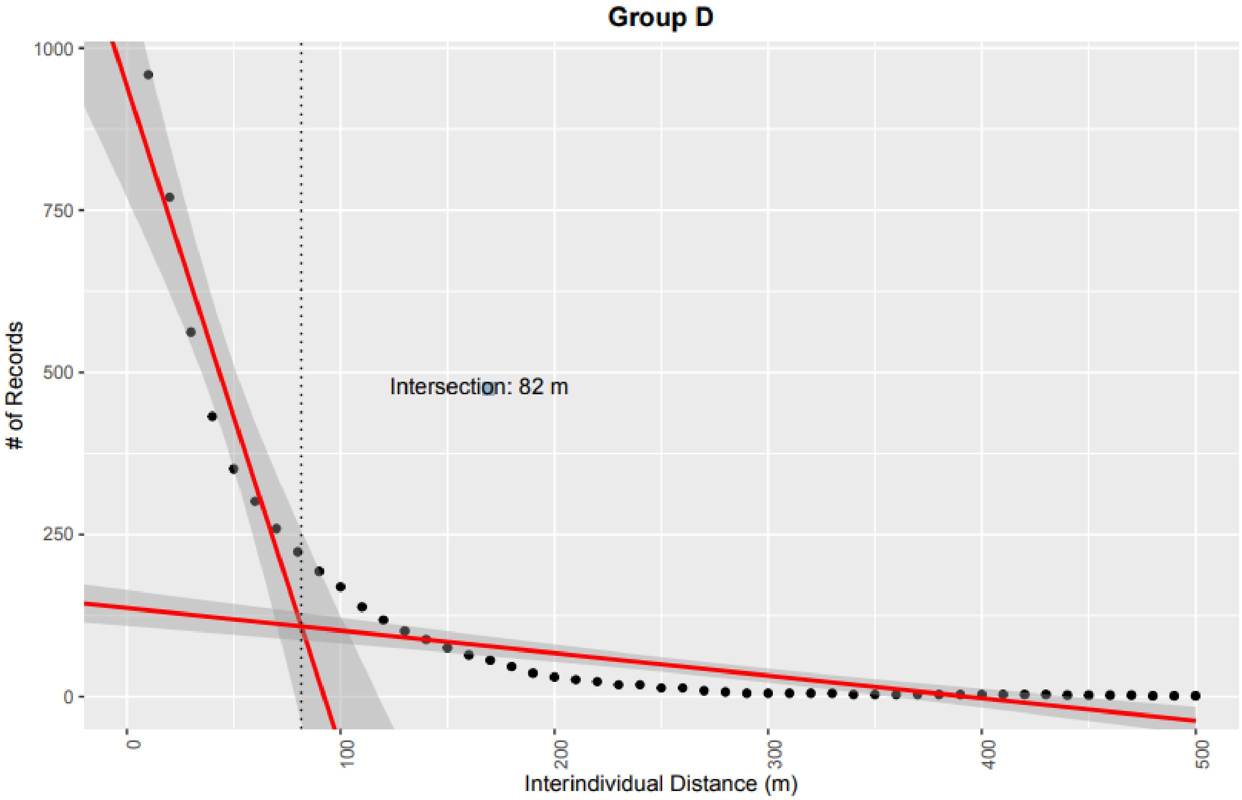


Figure 4.2 continued.

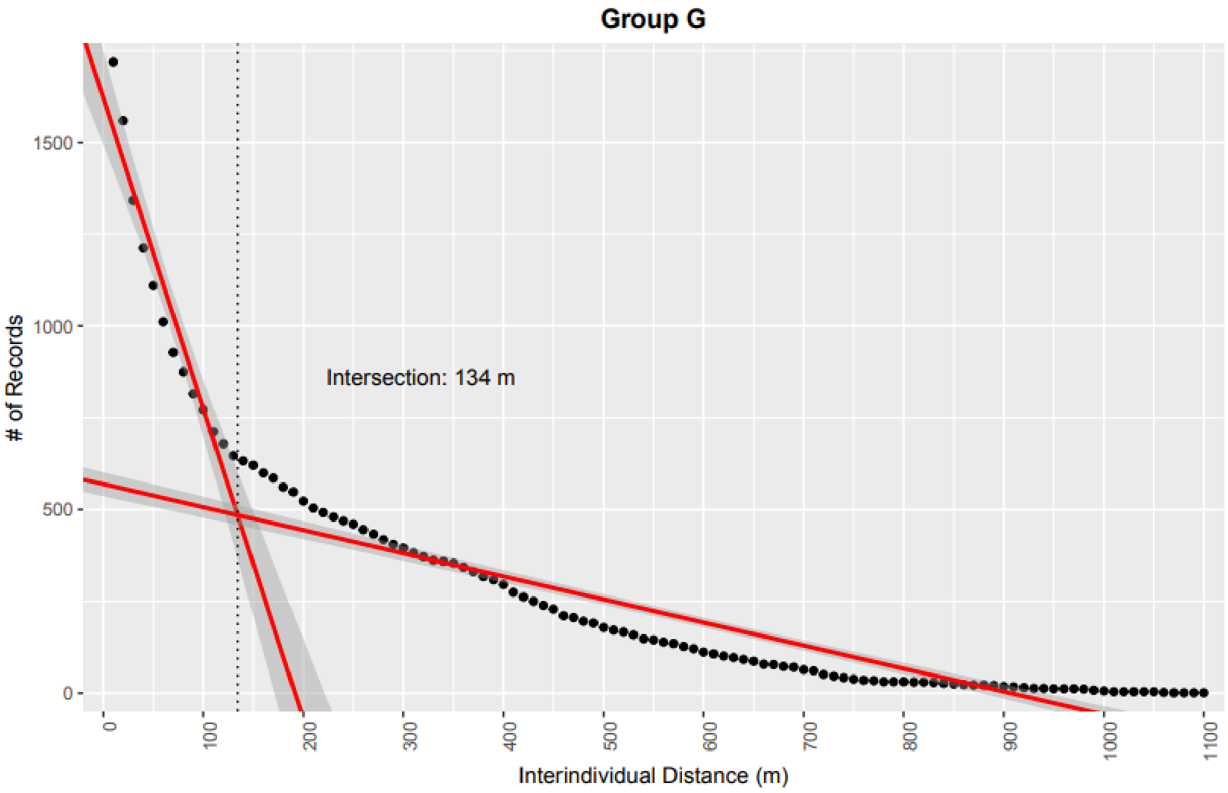
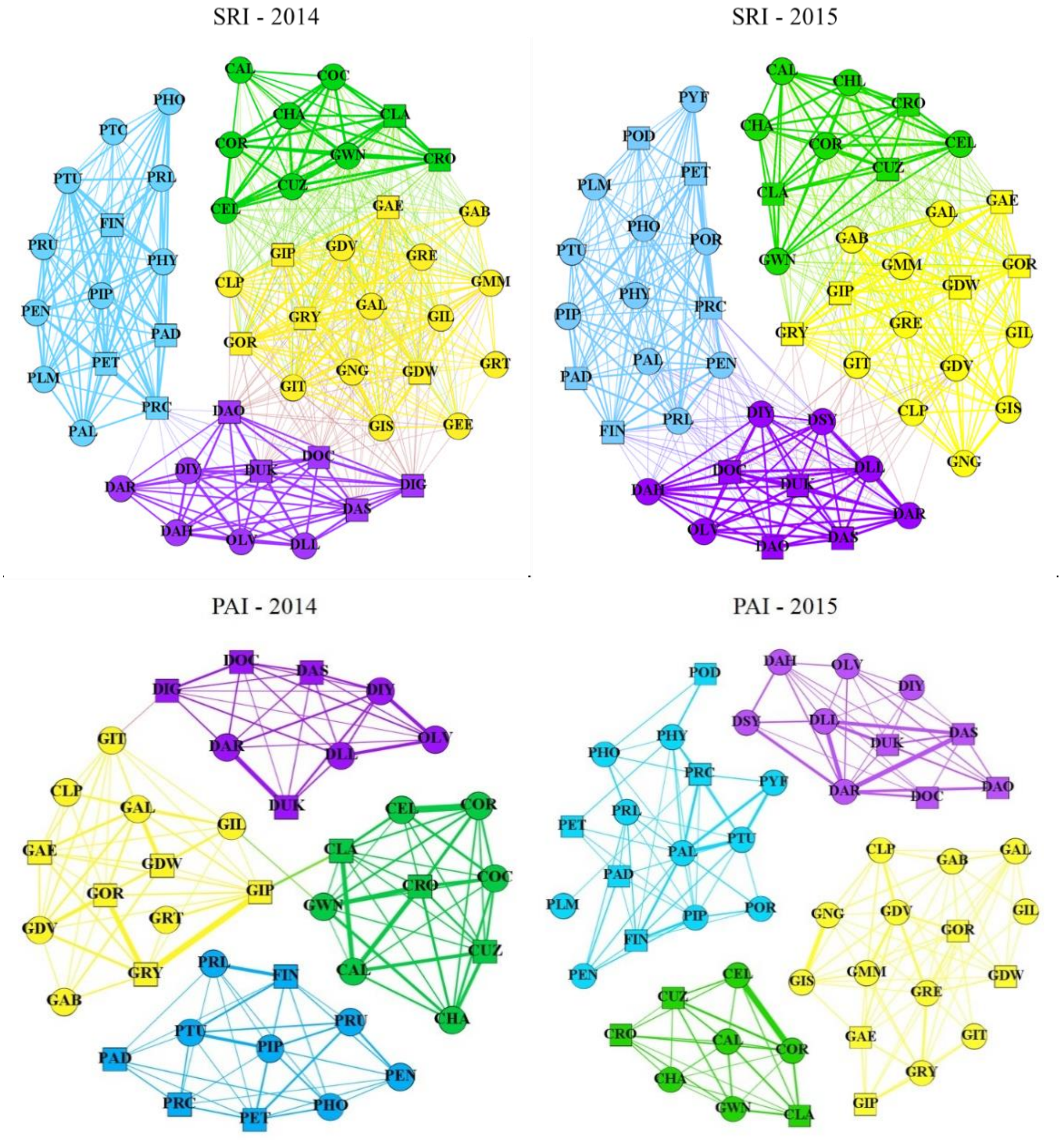


Figure 4.2 continued.

Figure 4.3. Social networks of 50 (2014) and 49 (2015) woolly monkeys, constructed from simple ratio indices (SRI) and proximity association indices (PAI). Lines represent associations between individuals, with thicker lines (higher edge weight) indicating higher association indices. Colors correspond to four social groups determined through hierarchical clustering and modularity scores (group C = green, group D = purple, group G = yellow, group P = blue). Networks based on party composition (SRI scores) exhibit many connections both within and between groups, while networks based on spatial proximity (PAI scores) are more sparse, with only a few individuals connected between groups in 2014, and no connections found between groups in 2014.


SRI - 2014

SRI - 2015

PAI - 2014

PAI - 2015

Figure 4.4. Results of hierarchical cluster analysis of simple ratio indices (SRI) using the the average linkage clustering method. Dendrograms for both the total network and adults only network of each association measure corresponding to each field season (2014 and 2015) are displayed. Animal pairs with higher association scores are found closer together. Each cluster is assigned a different color, with the corresponding group name displayed on the right. Below each dendrogram are the plots of cumulative bifurcations and maximum modularity. Cutoffs based on these methods are displayed with a dashed line. The black dashed line represents the association index that represents the maximum change in the rate of bifurcations (K) and the red dashed line represent the association index that maximizes modularity between clusters (M). Note that no significant rate of change in cumulative bifurcations was identified for the 2014 adult only network.

Figure 4.4 continued

A1) Dendrogram: SRI-2014 adults and subadults.

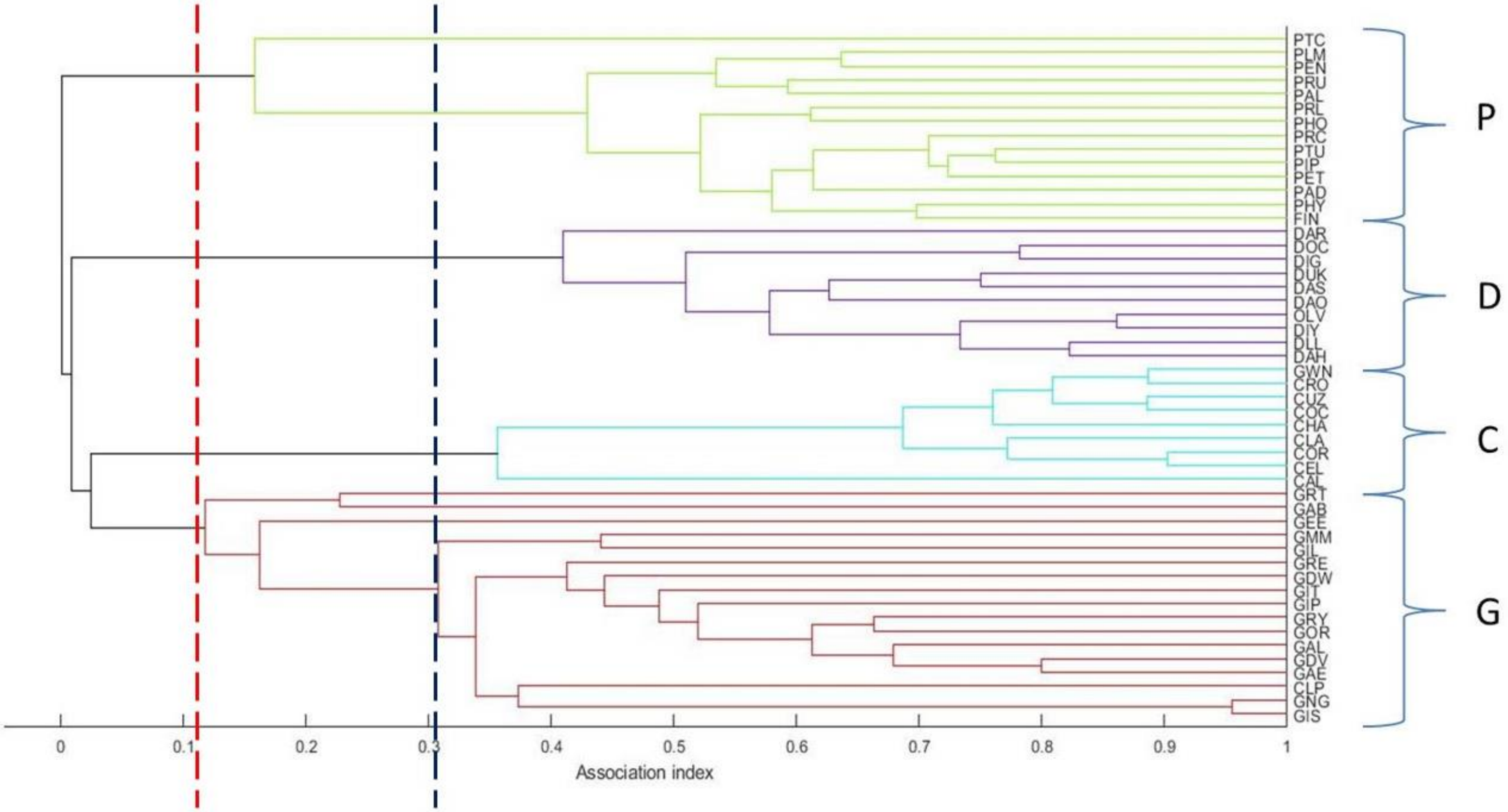


Figure 4.4 continued

A2) Cumulative bifurcation and maximum modularity diagrams: SRI-2014 adults and subadults.

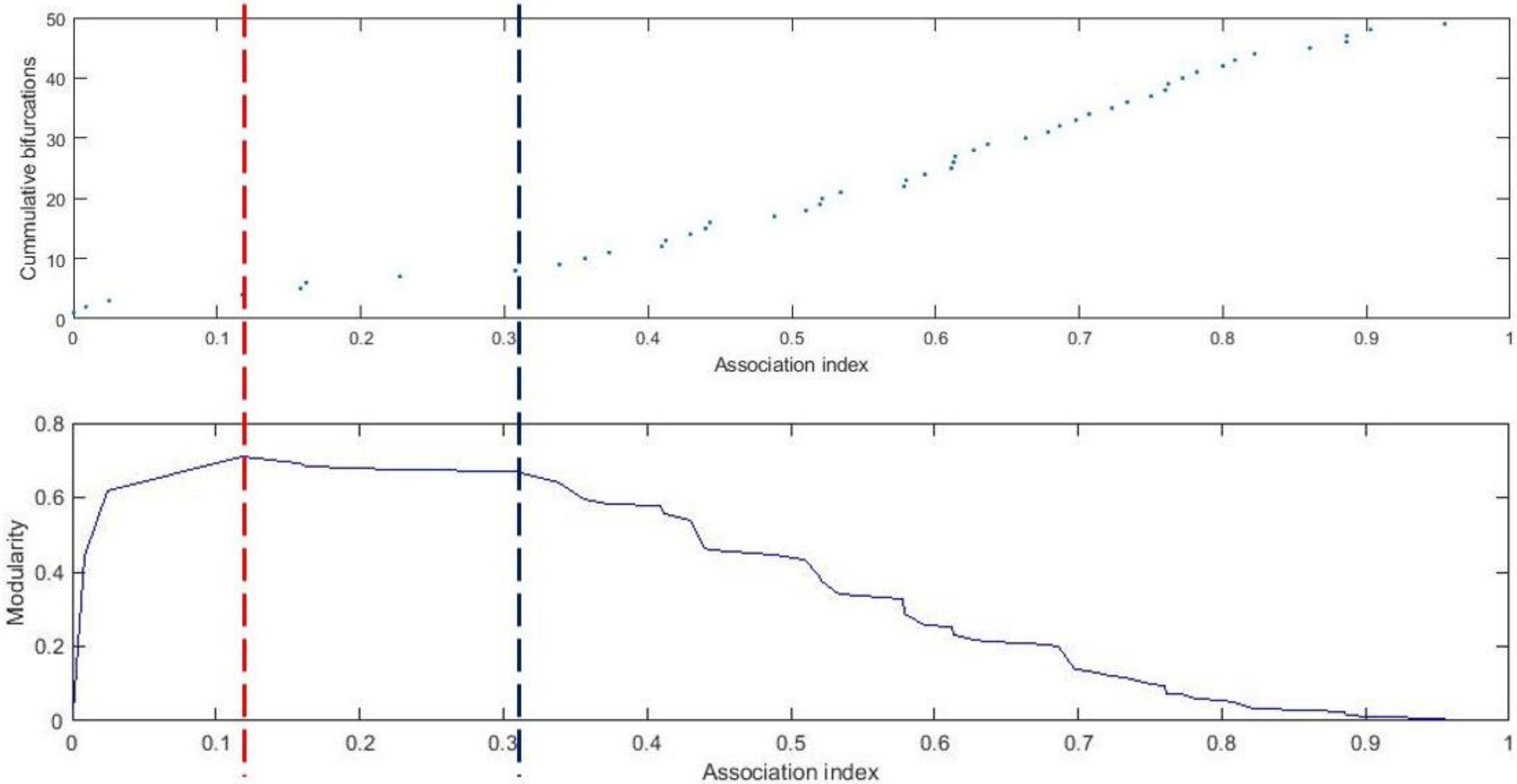


Figure 4.4 continued

B1) Dendrogram: SRI-2014 adults only.

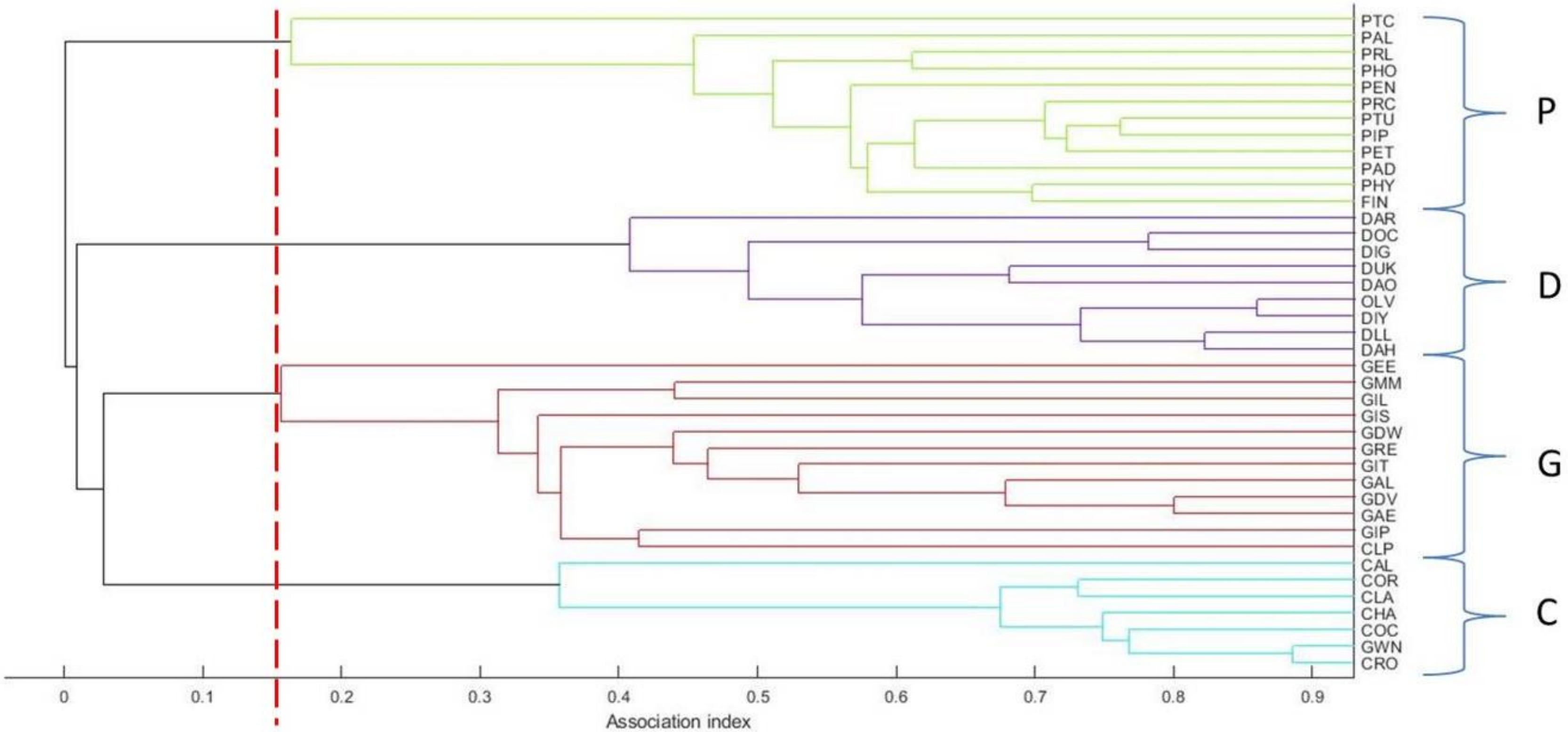


Figure 4.4 continued

B2) Cumulative bifurcation and maximum modularity diagrams: SRI-2014 adults only.

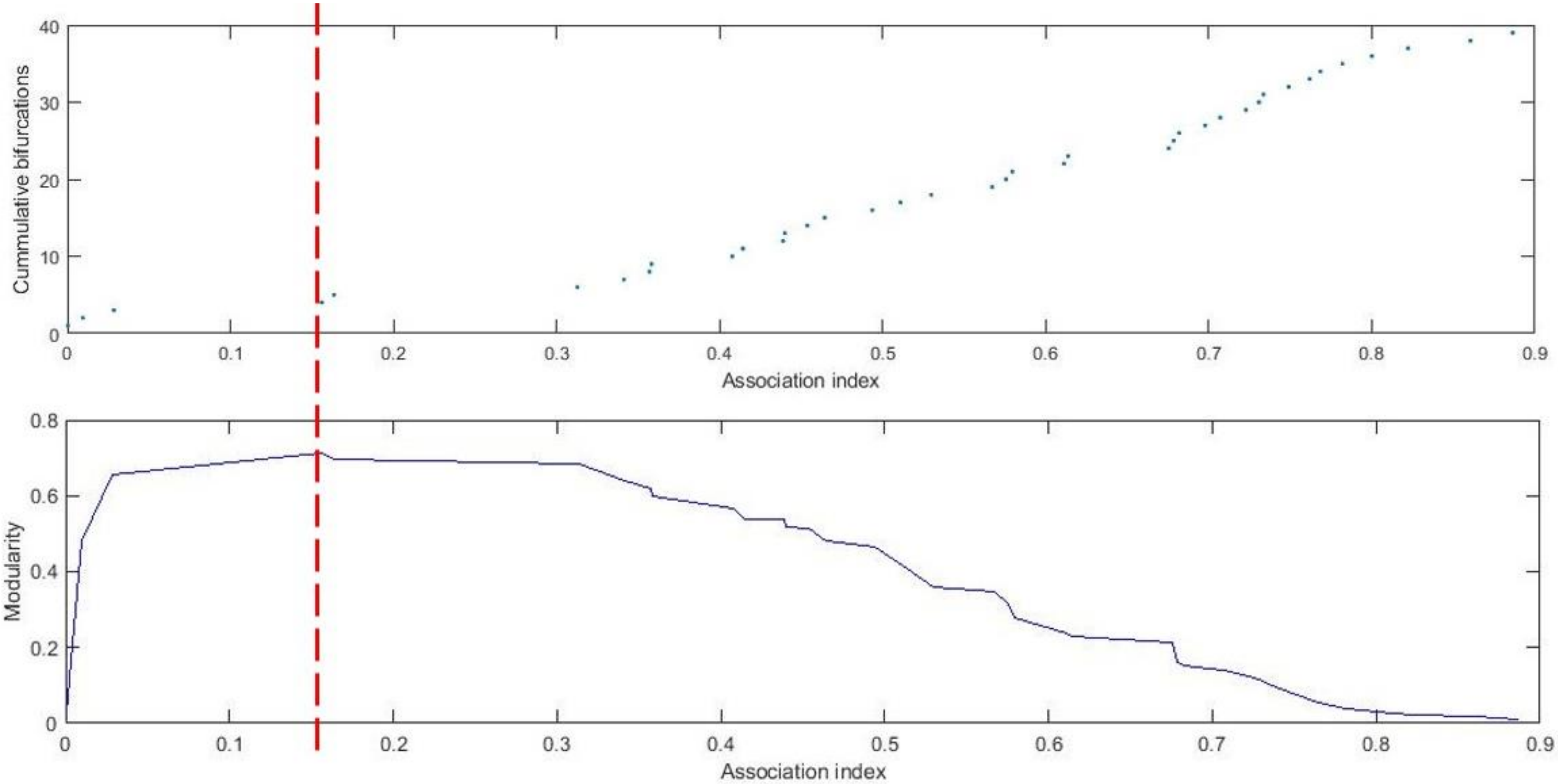


Figure 4.4 continued

C1) Dendrogram: SRI-2015 adults and subadults.

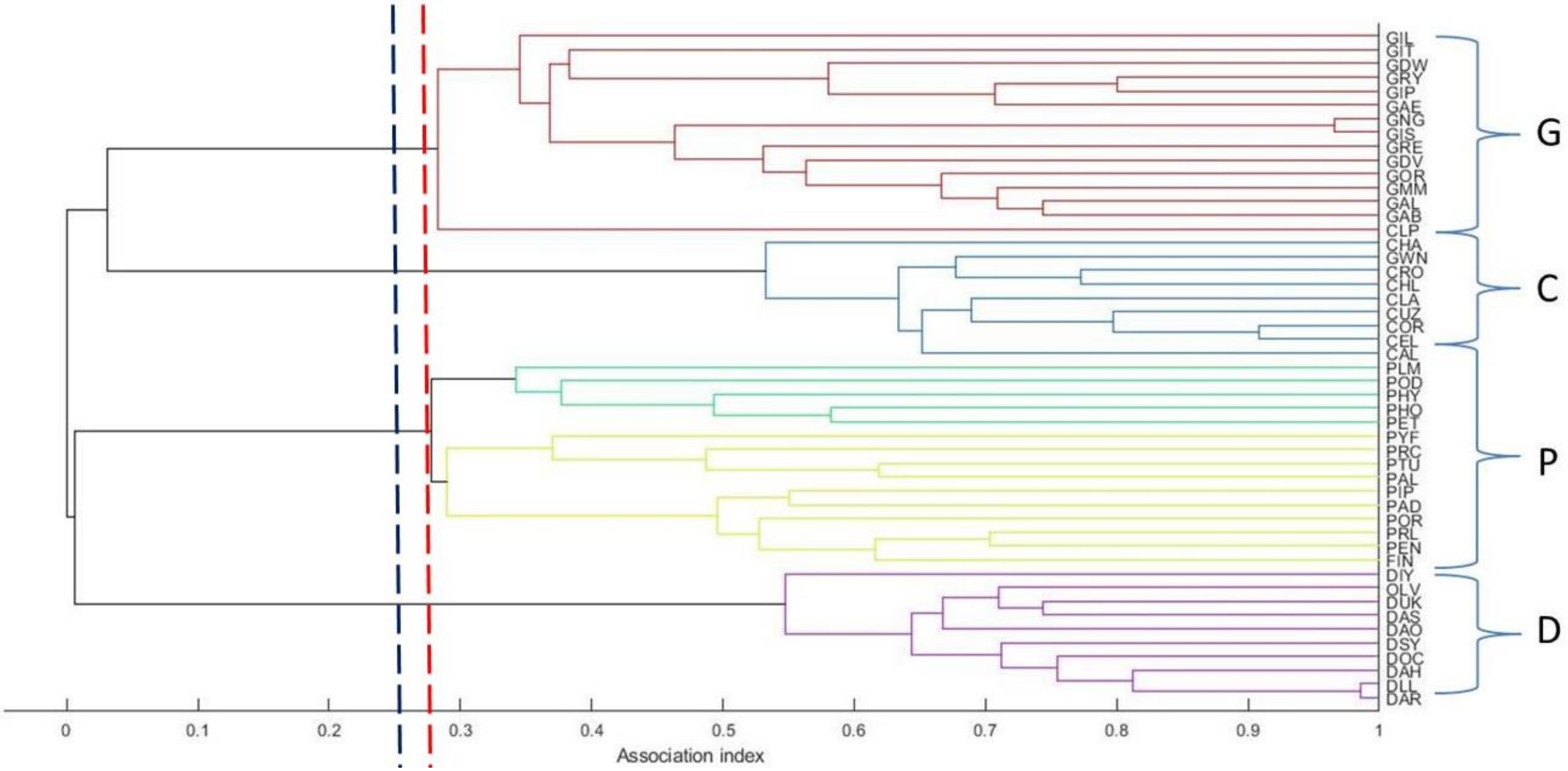


Figure 4.4 continued

C2) Cumulative bifurcation and maximum modularity diagrams: SRI-2015 adults and subadults.

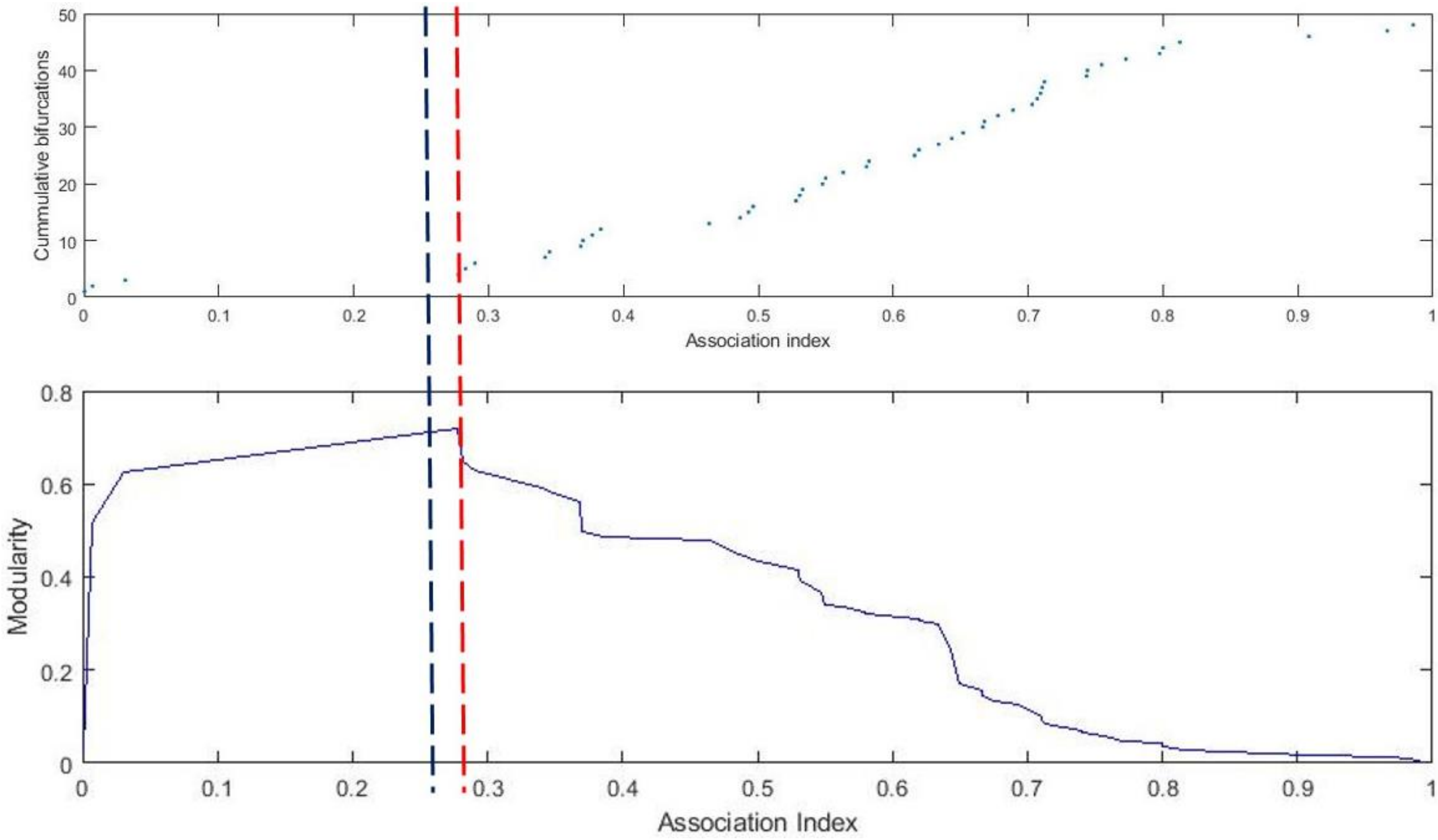


Figure 4.4 continued

D1) Dendrogram: SRI-2015 adults only.

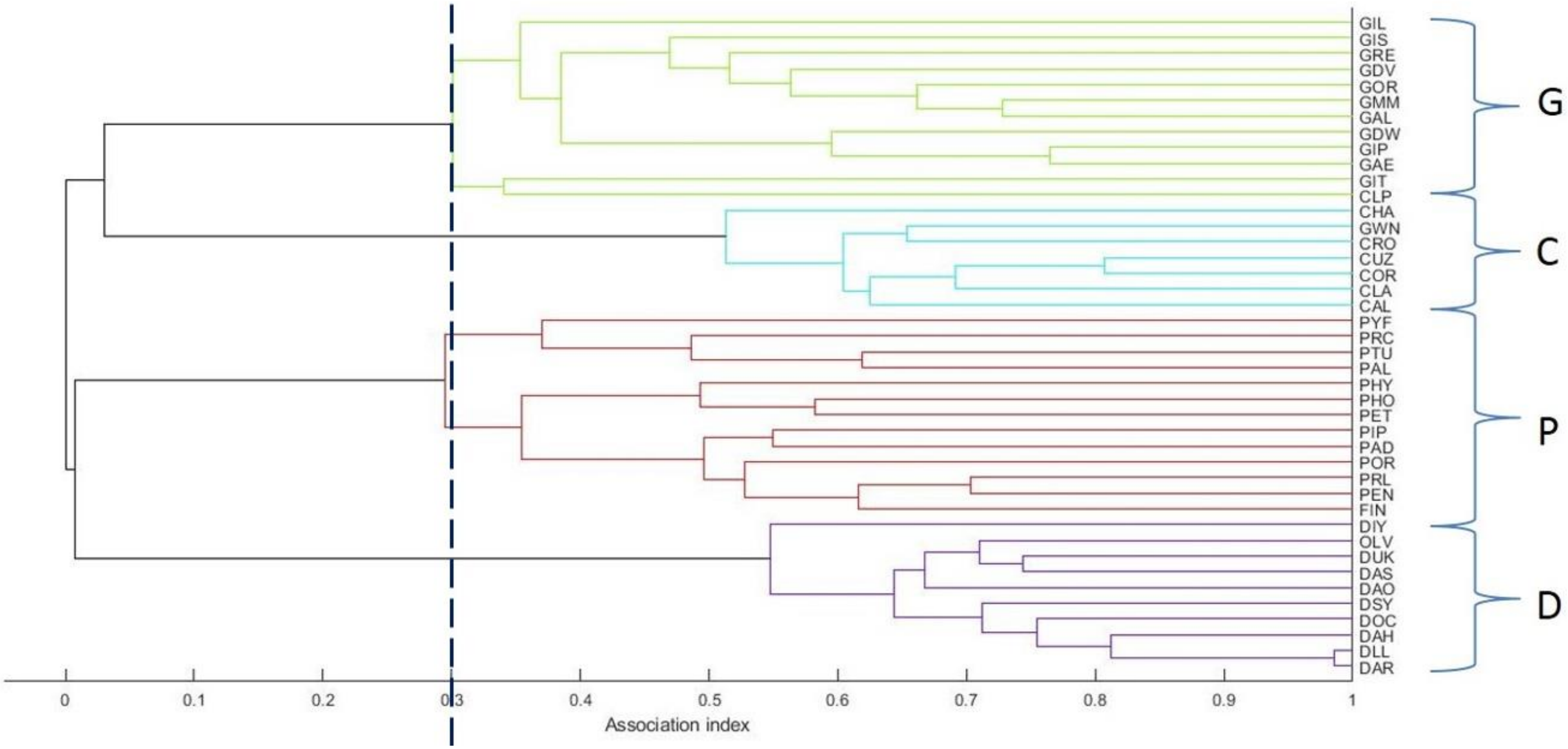


Figure 4.4 continued

D2) Cumulative bifurcation and maximum modularity diagrams: SRI-2015 adults only.

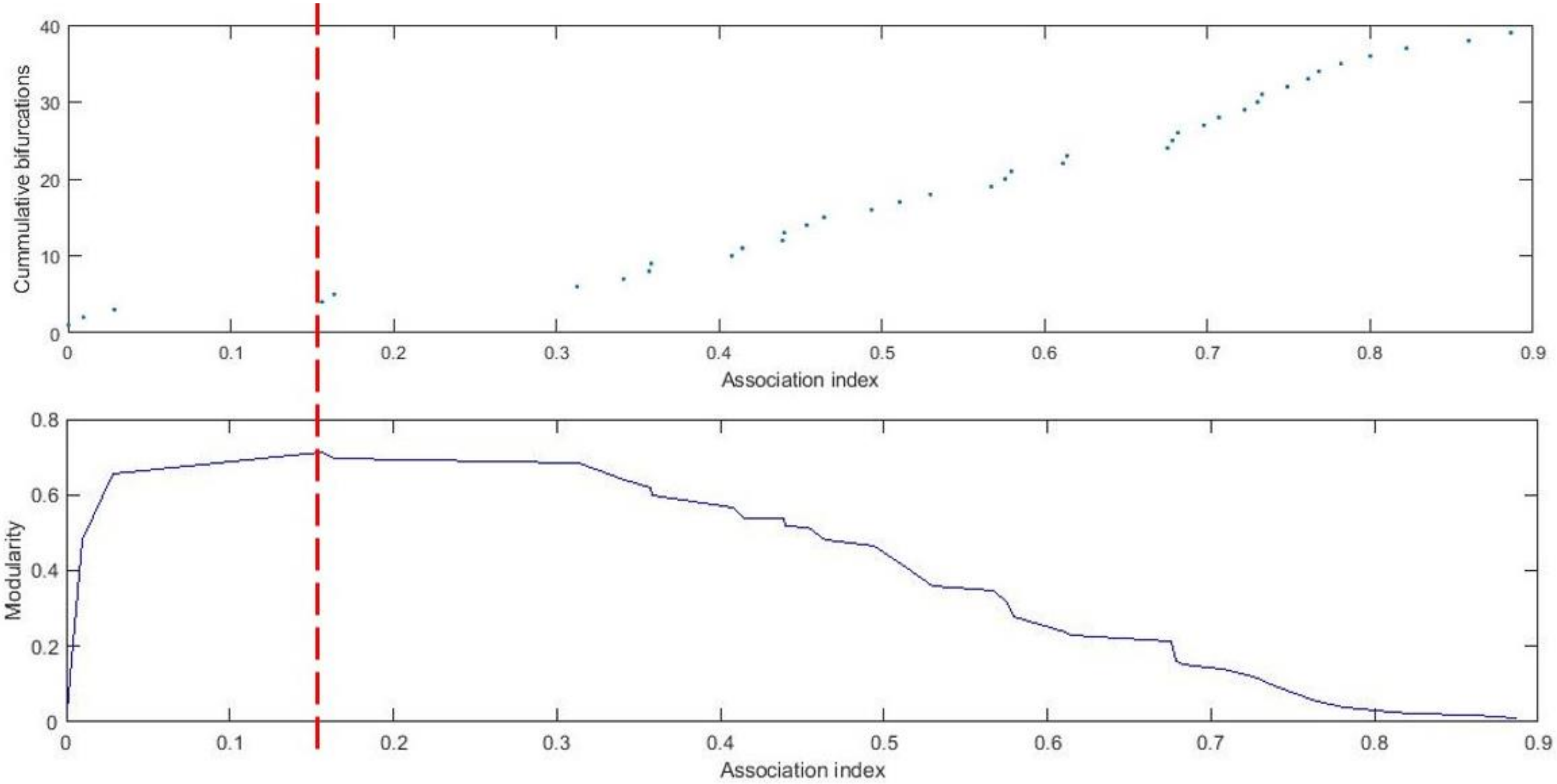


Figure 4.5. Results of hierarchical cluster analysis of proximity association indices (PAI) using the average linkage clustering method. Dendrograms for both the total network and adults only network of each association measure corresponding to each field season (2014 and 2015) are displayed. Animal pairs with higher association scores are found closer together. Each cluster is assigned a different color, with the corresponding group name displayed on the right. Below each dendrogram are the plots of cumulative bifurcations and maximum modularity. Cutoffs based on these methods are displayed with a dashed line. The black dashed line represents the association index that represents the maximum change in the rate of bifurcations (K) and the red dashed line represent the association index that maximizes modularity between clusters (M). Note that when subadults are removed, clustering is more apparent, and in 2014 several of the closest associations (DUK-DAR, CRO-GWN, CLA-CAL) are between males and receptive females that were known to give birth in 2015.

Figure 4.5 continued

A1) Dendrogram: PAI-2014 adults and subadults.

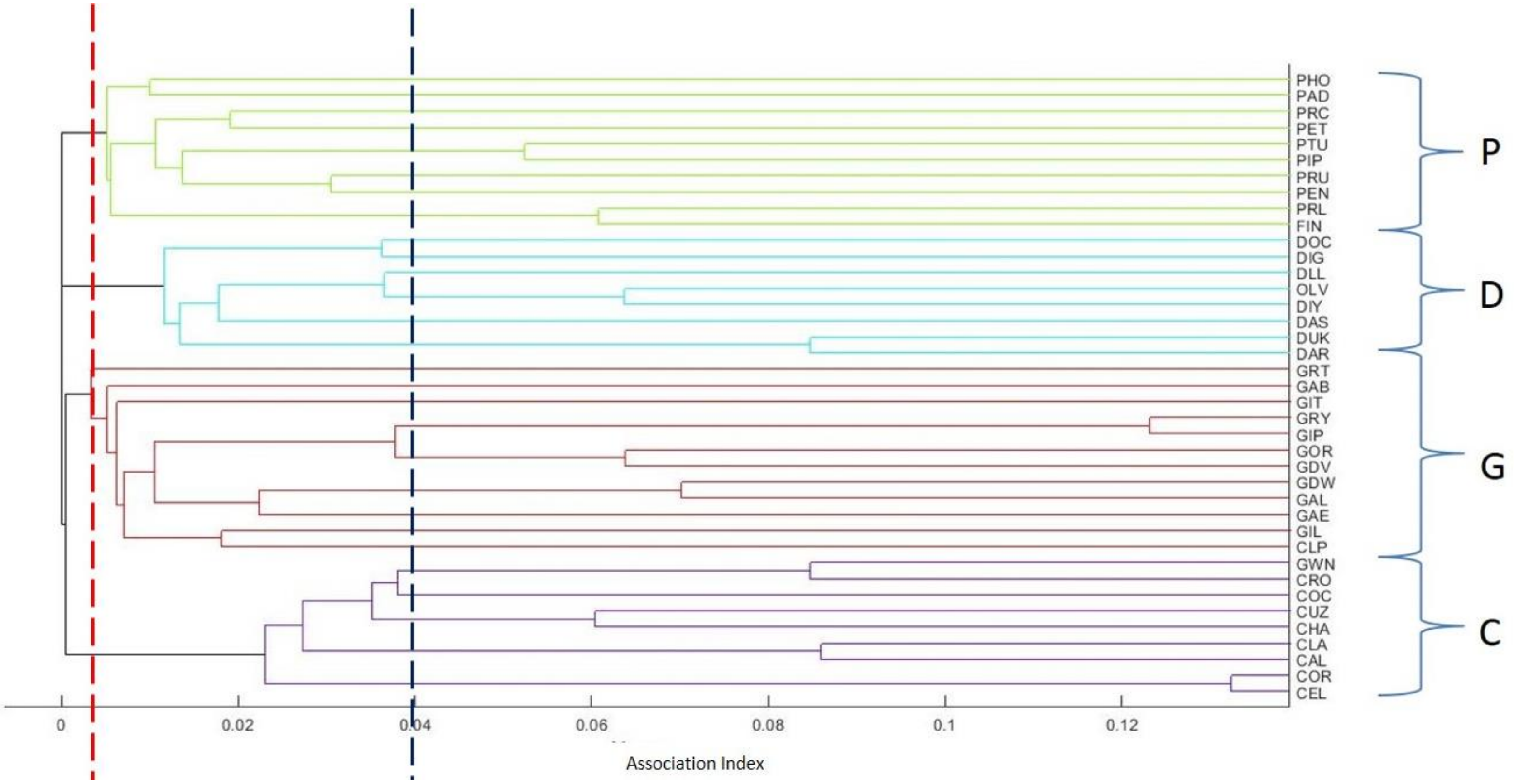


Figure 4.5 continued

A2) Cumulative bifurcation and maximum modularity diagrams: PAI-2014 adults and subadults.

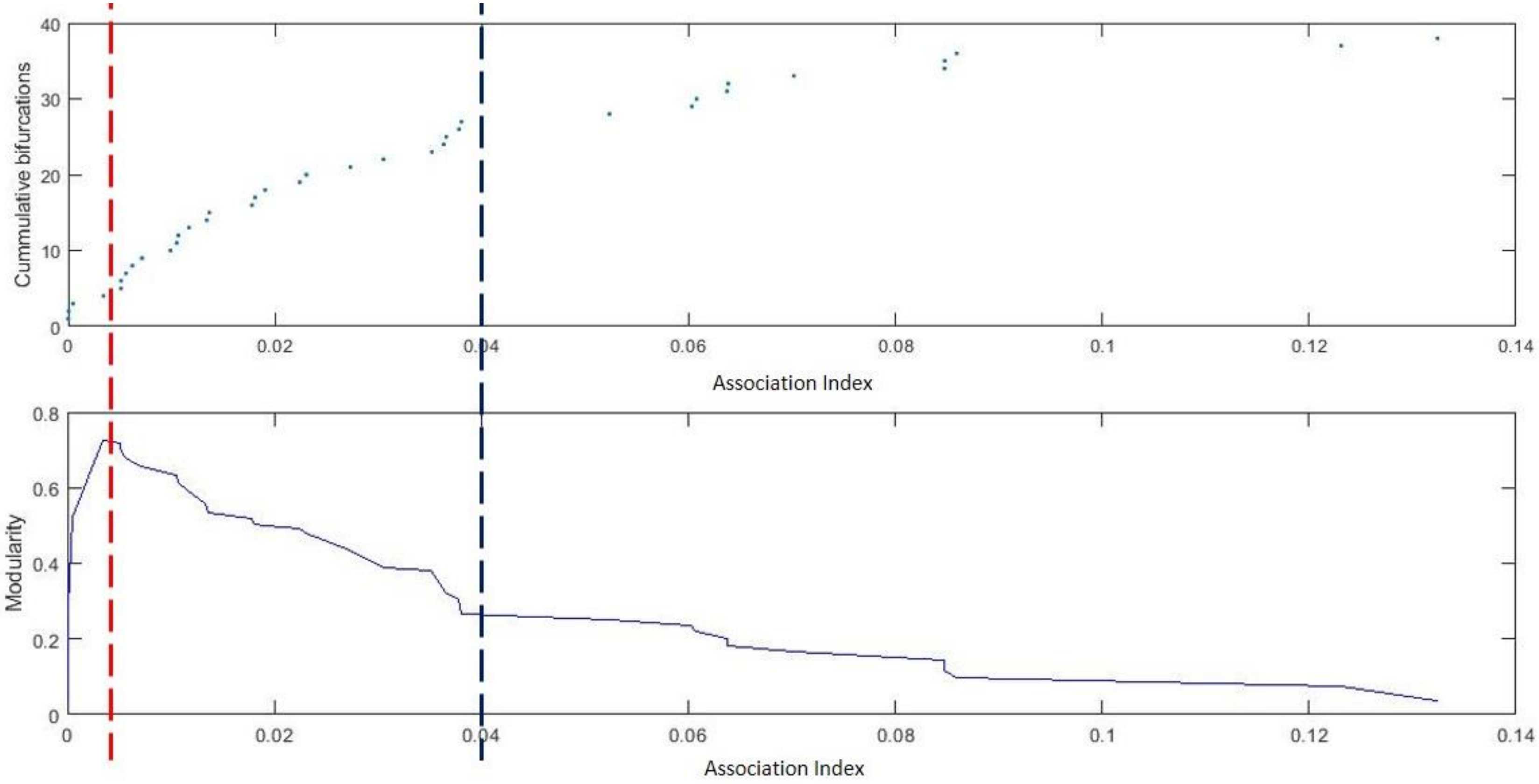


Figure 4.5 continued

B1) Dendrogram: PAI-2014 adults only.

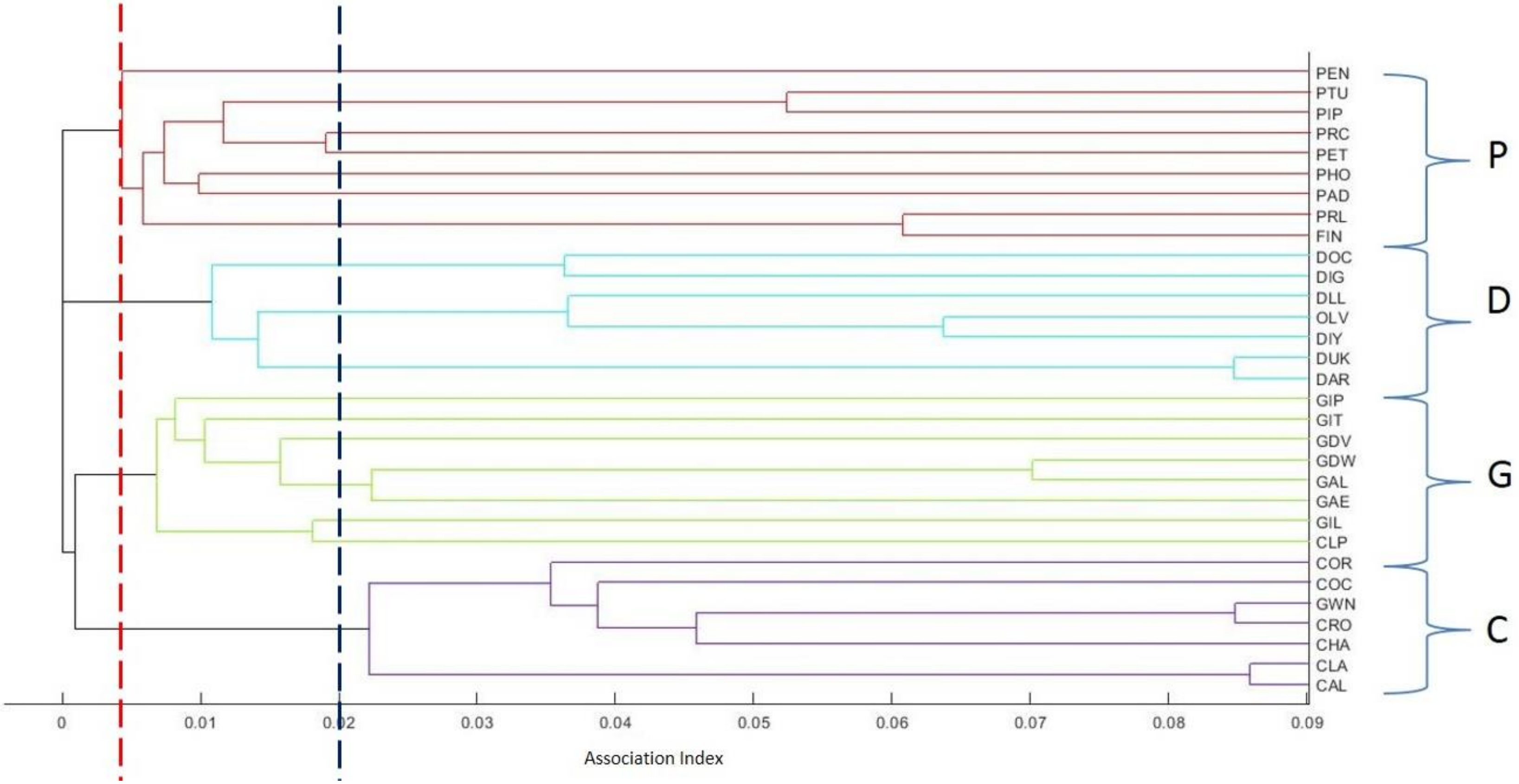


Figure 4.5 continued

B2) Cumulative bifurcation and maximum modularity diagrams: PAI-2014 adults only.

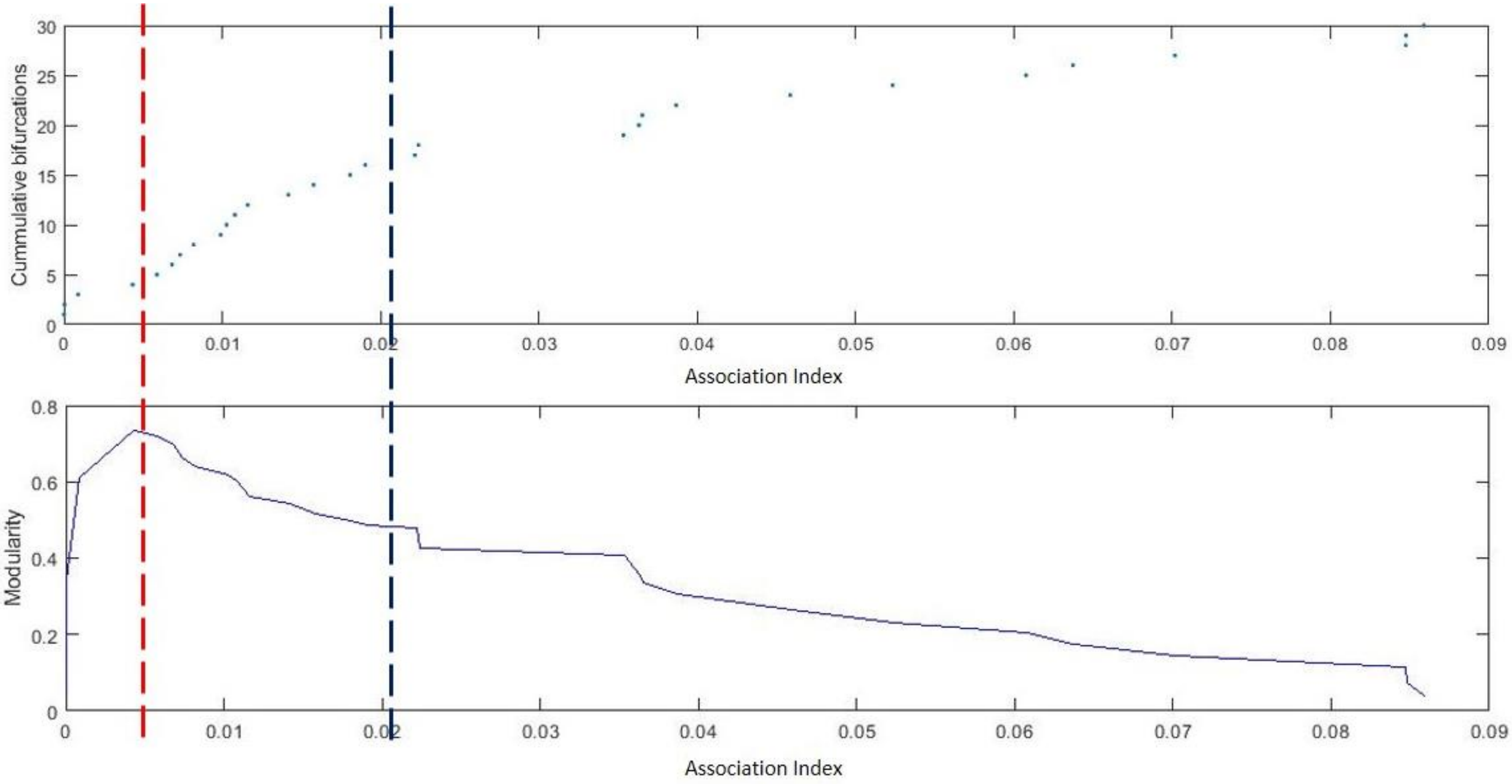


Figure 4.5 continued

C1) Dendrogram: PAI-2015 adults and subadults.

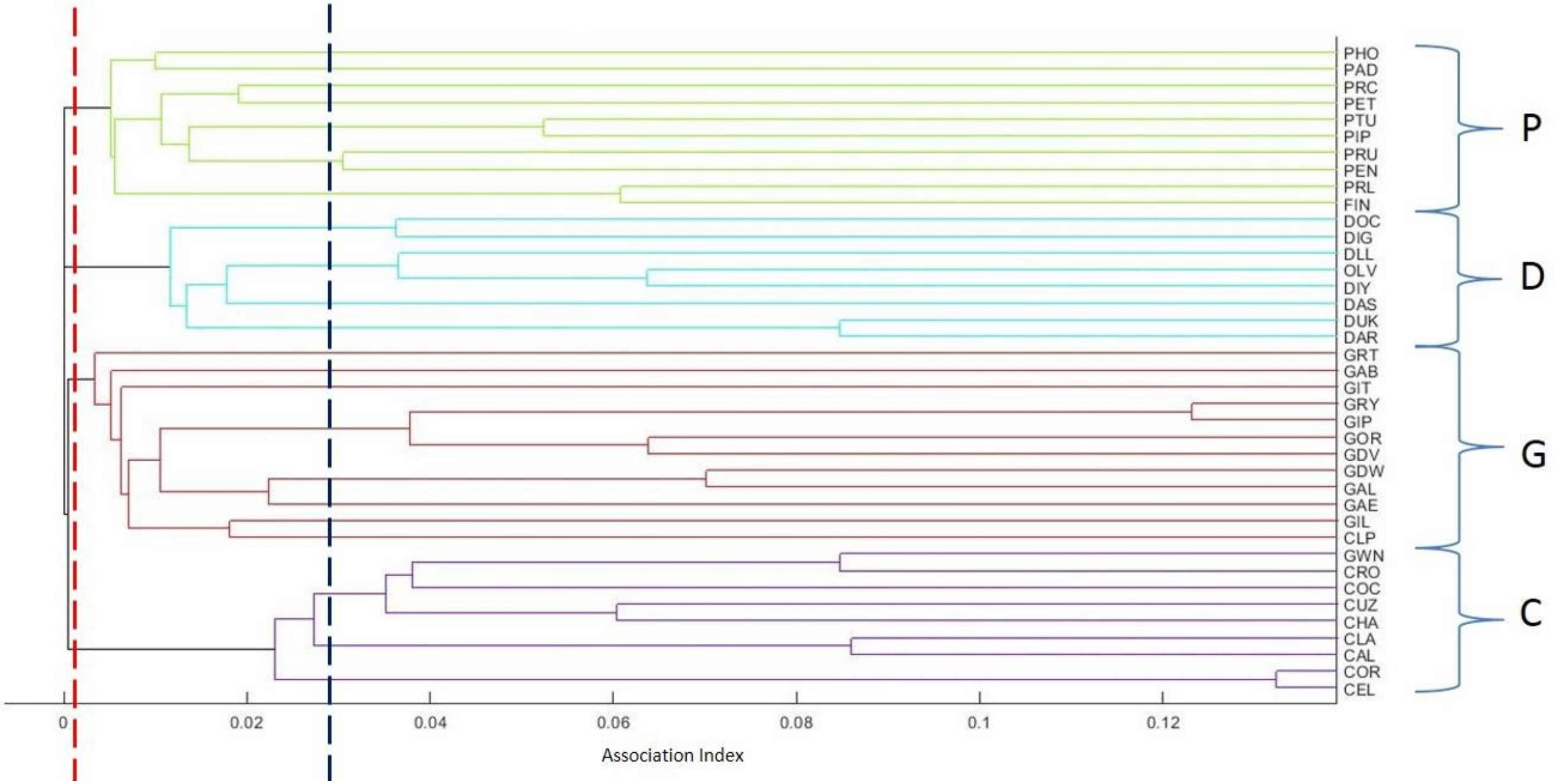


Figure 4.5 continued

C2) Cumulative bifurcation and maximum modularity diagrams: PAI-2015 adults and subadults.

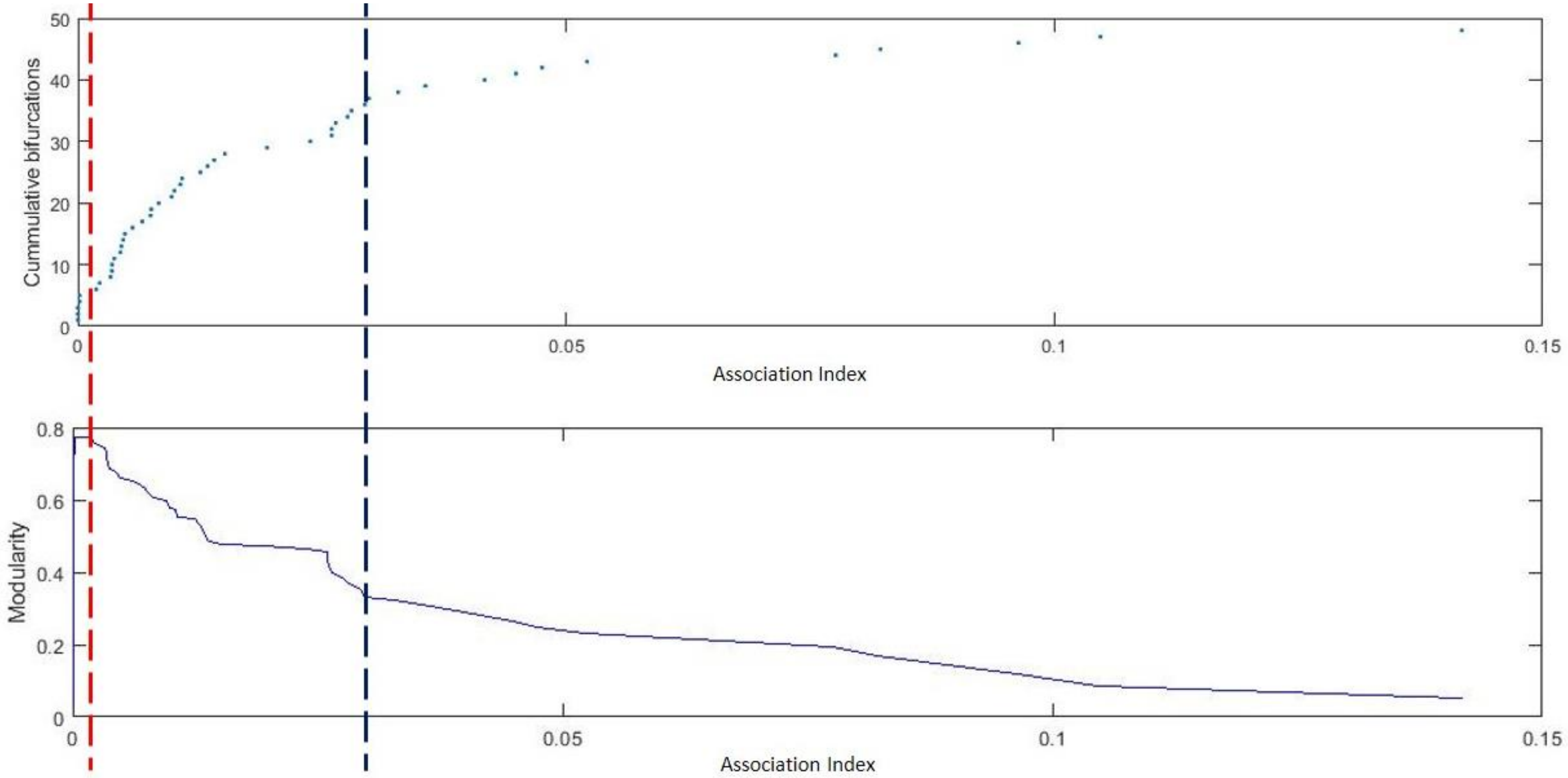


Figure 4.5 continued

D1) Dendrogram: PAI-2015 adults only.

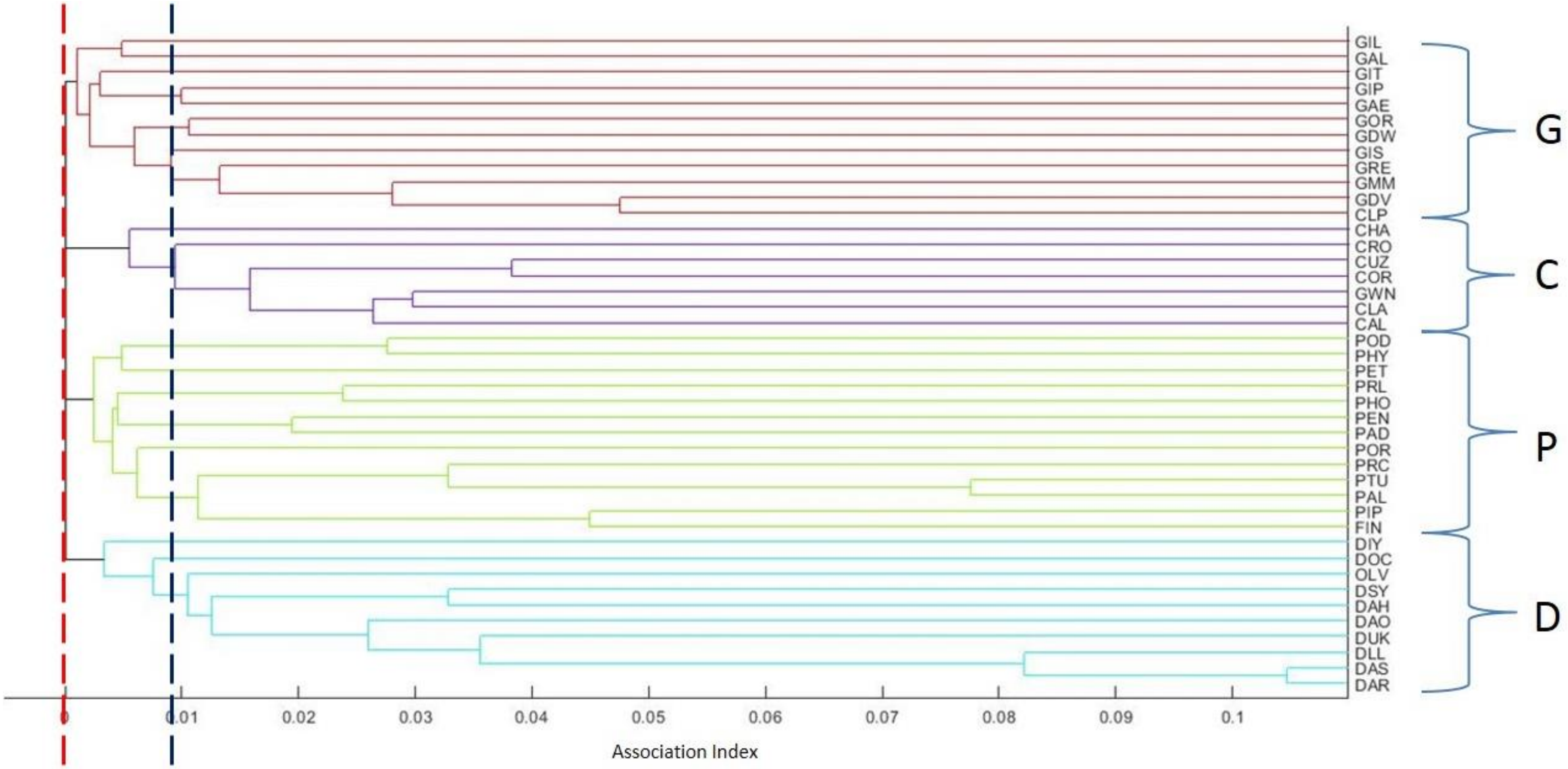


Figure 4.5 continued

D2) Cumulative bifurcation and maximum modularity diagrams: PAI-2015 adults only.

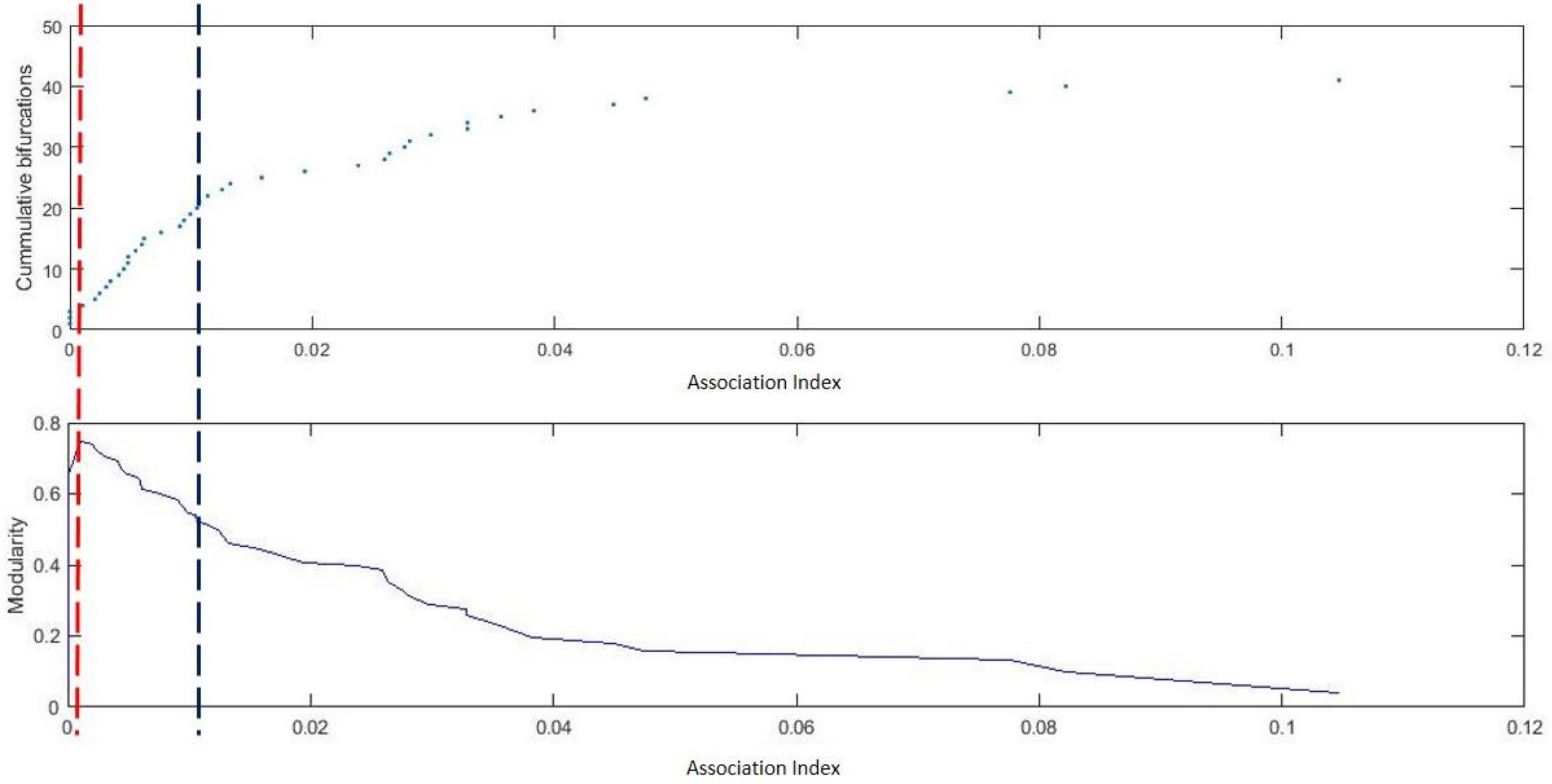


Figure 4.6. Average and range in simple ratio index (SRI) scores for individual woolly monkeys assigned to 4 social groups by hierarchical cluster analysis in two field seasons (2014 left, 2015 right) compared to the average SRI score of individuals that associated between those groups (red dotted line).

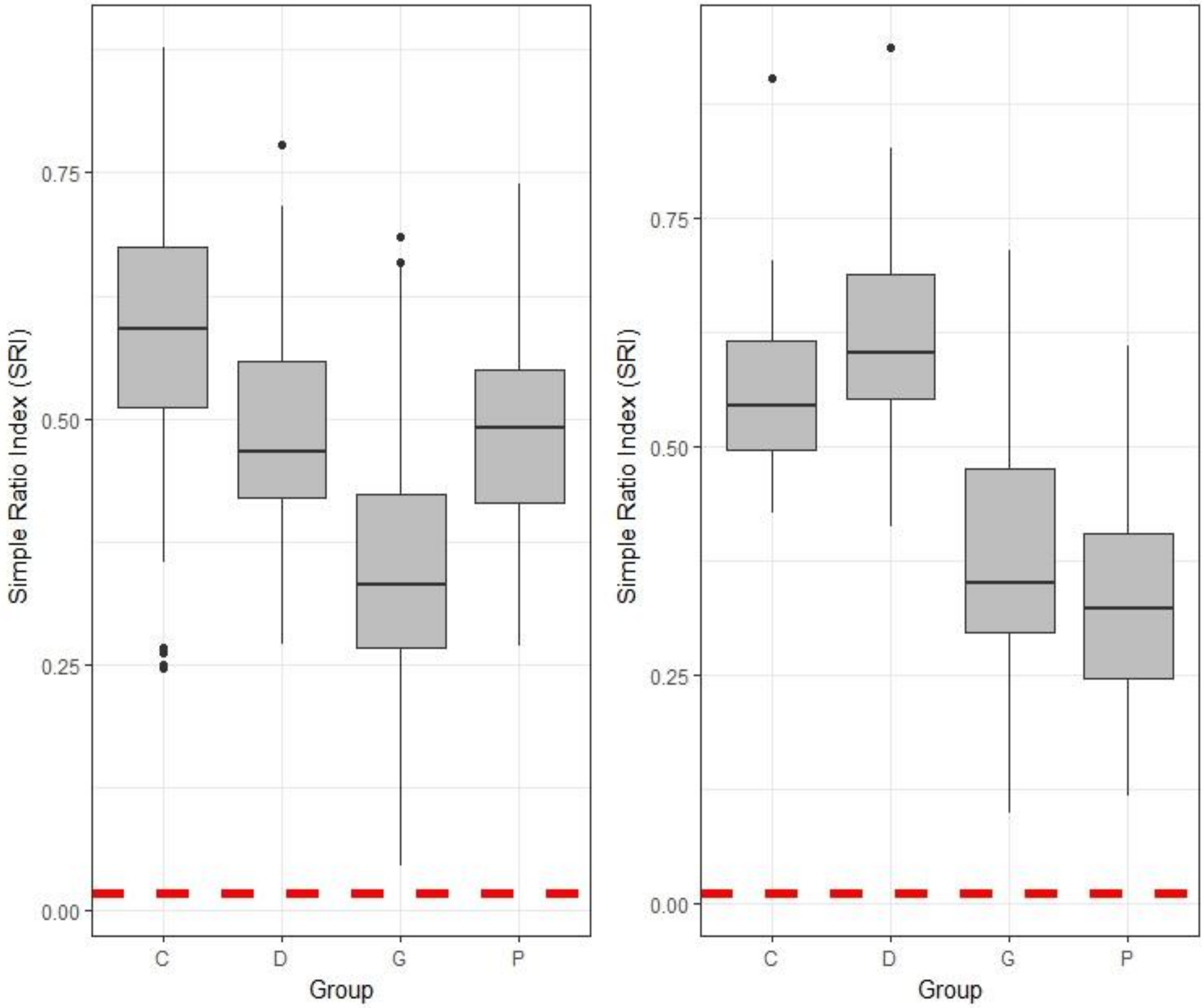


Figure 4.7. Boxplots of estimated Queller-Goodnight relatedness coefficients among female-female dyads (F-F), female-male dyads (M-F), and male-male dyads (M-M) within four social groups of woolly monkeys.

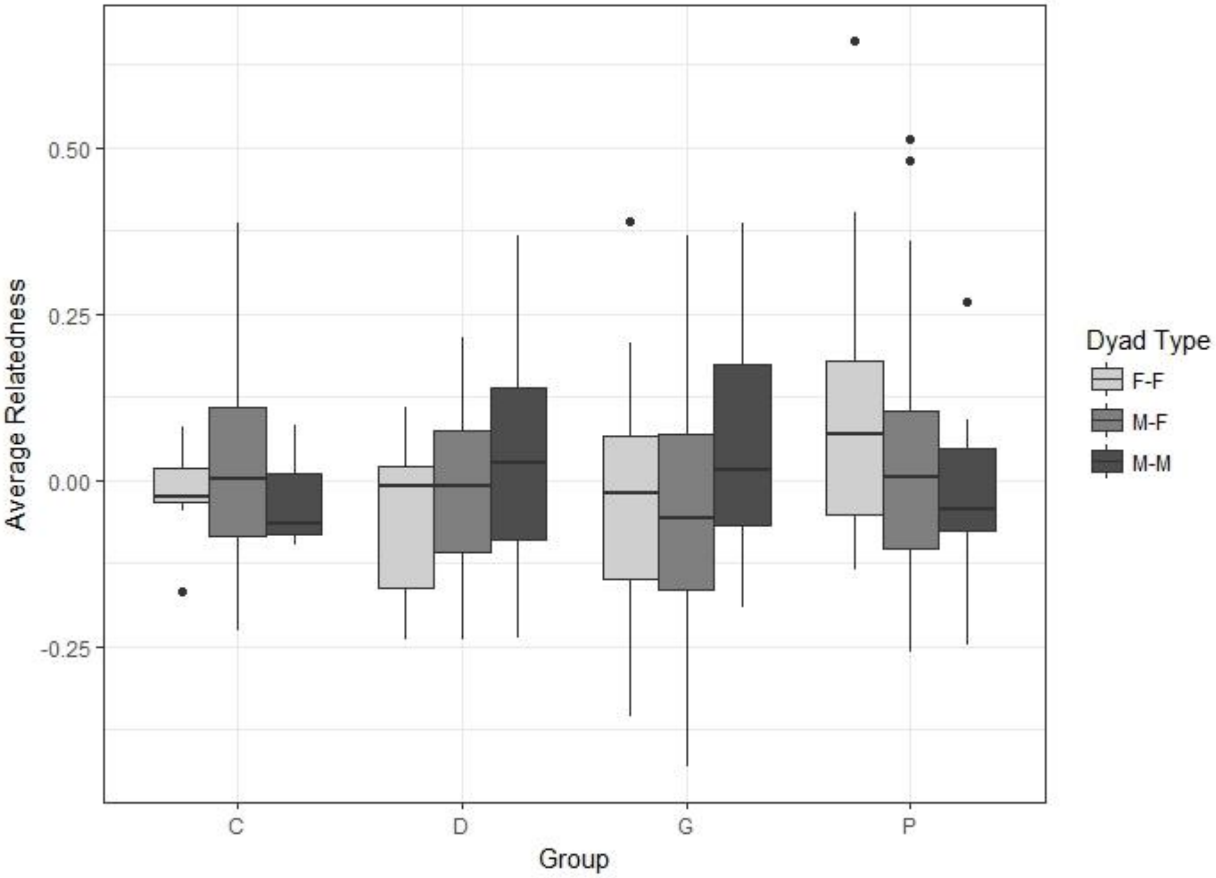


Figure 4.8. Network depicting estimated pairwise genetic relatedness among all adults (N = 46) and subadults (N = 5) sampled from four putative social groups of woolly monkeys between 2014 and 2015. Edges represent inferred first order relatives (parent-offspring, full-sibling, and half-sibling pairs, based on likelihood ratio tests between the null hypothesis of unrelated and alternative hypothesis of one of these relatedness categories, as implemented in KINGROUP 2 [Konovolov et al. 2004]). Colors represent the social group within which the individual noted was sampled and was resident during the 2014 and 2015 field seasons (Group C = green, Group D = purple, Group G = yellow, Group P = blue).

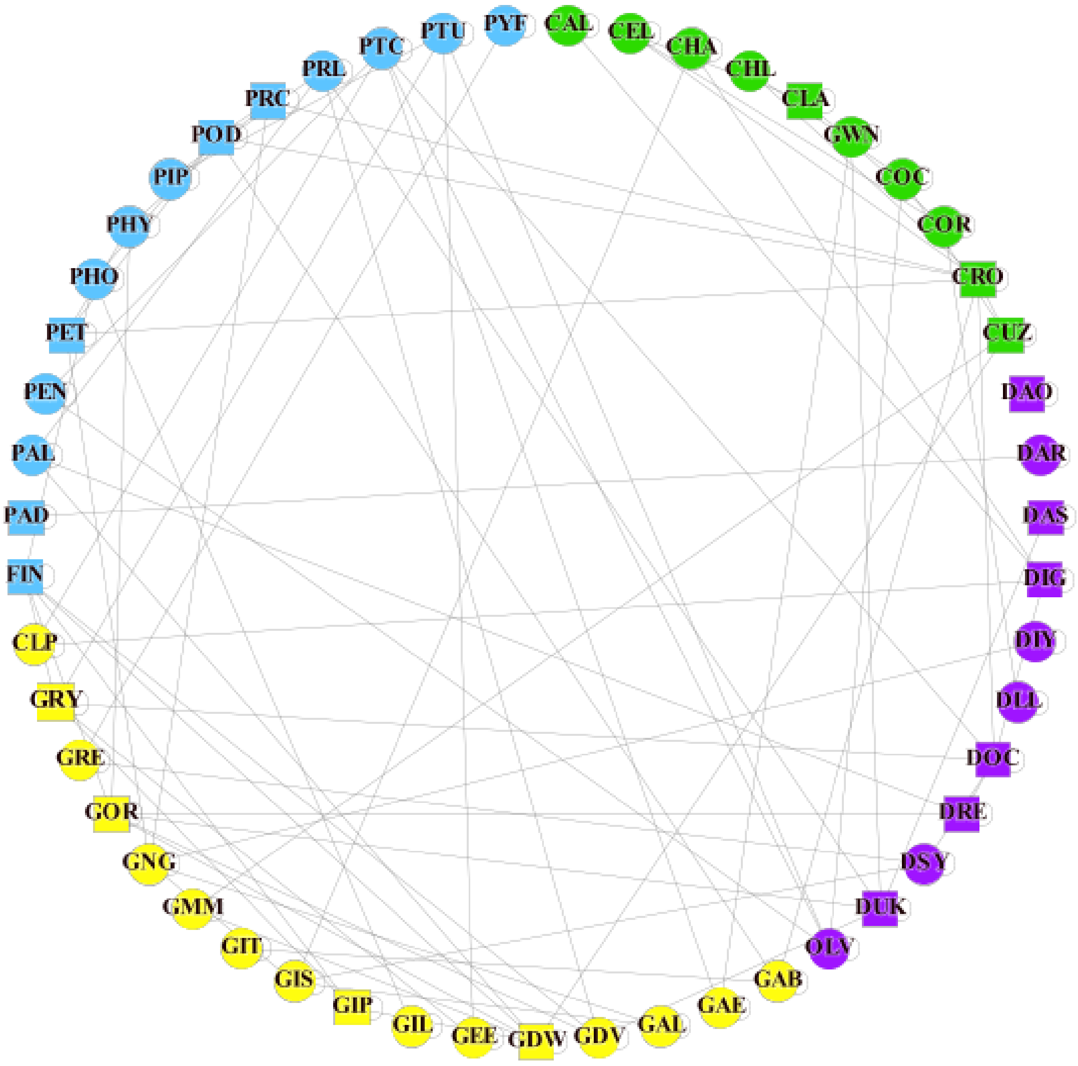


Figure 4.9. Simple ratio indices (SRI) among female-female dyads, female-male dyads, and male-male dyads. Male-male dyads had significantly higher SRIs in 2015 than other dyad types (p < 0.003 versus female-female dyads, and p<0.003 versus male female dyads).

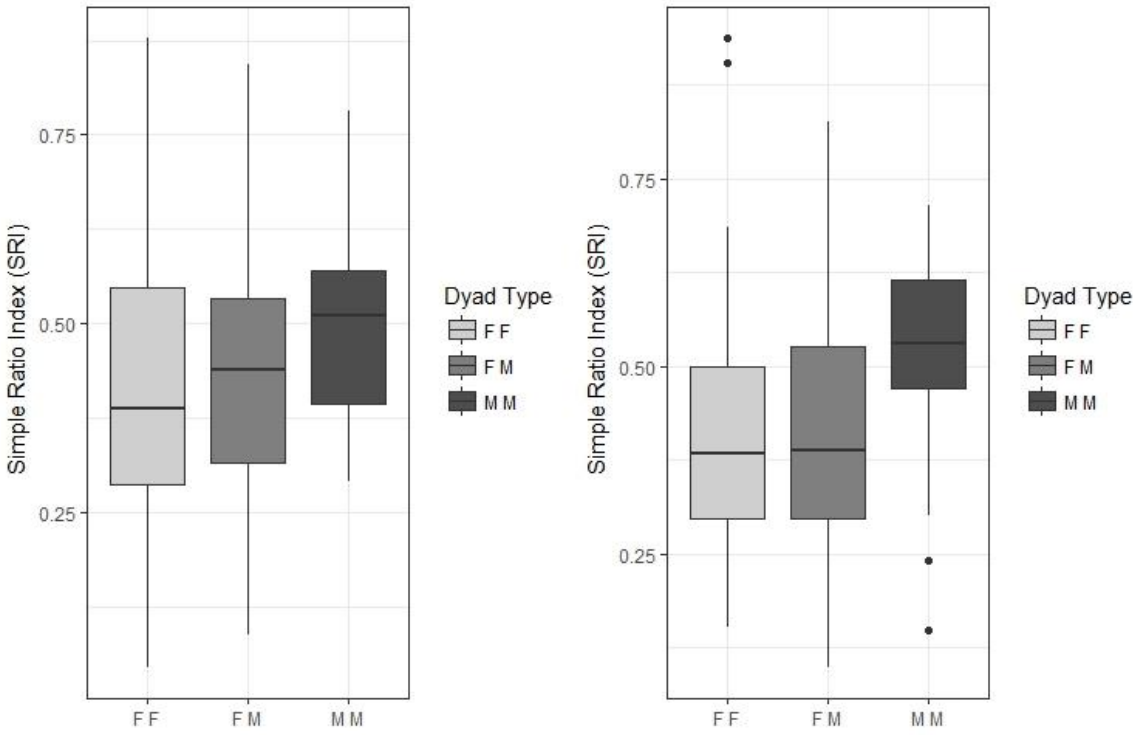
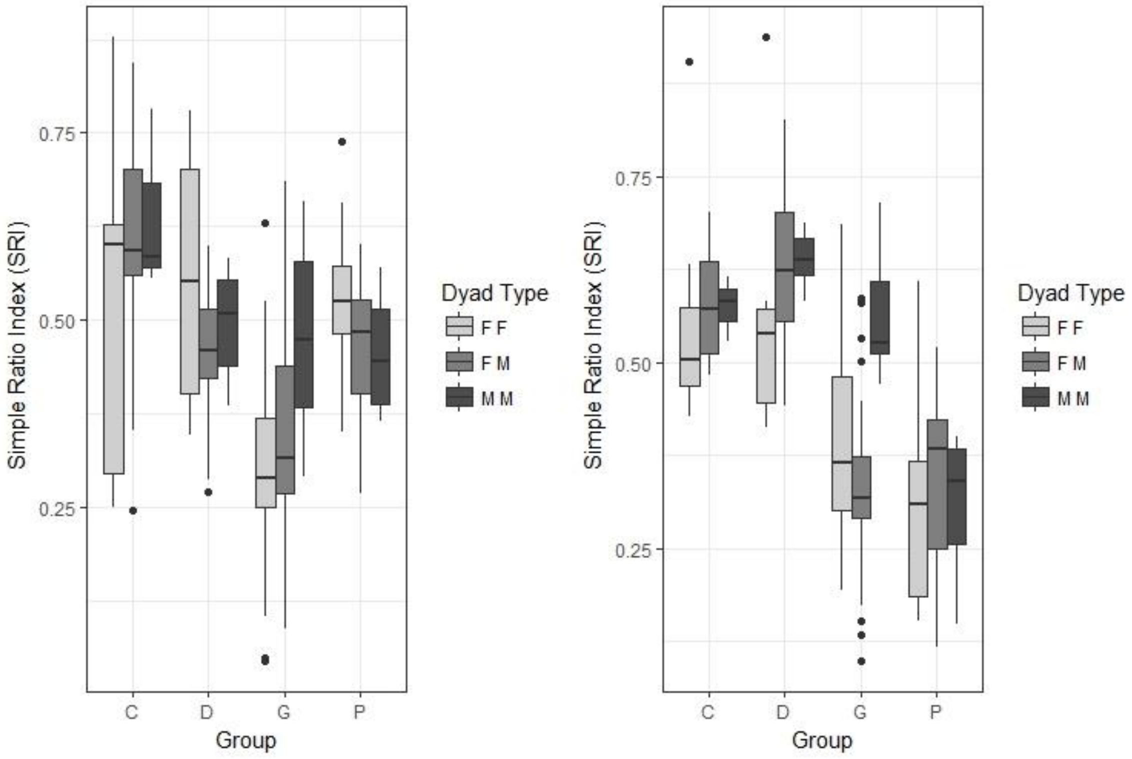


Figure 4.10. Average and range in simple ratio index (SRI) scores for female-female, female-male, and male-male dyads within 4 social groups of woolly monkeys in two field seasons (2014 left, 2015 right).



Chapter 5: Summary and Conclusions

This dissertation investigated several factors thought to influence the ranging patterns and grouping dynamics of lowland woolly monkeys at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador. My main objective was to quantitatively assess variation in range use and spatiotemporal associations of individually recognized woolly monkeys across multiple social groups and determine how that variation relates to habitat wide estimates of fruit availability, mating opportunities, and genetic relatedness. A second major aim was to use measures of spatial association patterns among recognized individuals, within and between social groups, to provide a quantitative description of woolly monkey social structure, as prior fieldwork had suggested interesting and enigmatic complexity to this structure (Kavanaugh and Dresdale 1975; Nishimura 1990; Defler and Defler 1995; Peres 1996; Di Fiore 1997, 2005). Here, I summarize the major contributions of my work, discuss the limitations of my dataset, and outline a few areas for productive future research.

In **Chapter 2**, I provided some of the first reported data on the reproductive patterns of wild woolly monkeys (and sympatric white-bellied spider monkeys) from the western Amazon, and I examined how the timing of reproductive events (e.g., copulations, conceptions, and births) relate to habitat wide estimates of ripe fruit availability, a preferred resource for both taxa. Given the slow life histories and long-periods of infant dependency in large-bodied atelin primates, long-term data is critical to our understanding of reproductive strategies and sexual behavior in this clade. Yet, longitudinal data on wild populations of atelins is still relatively scarce, making this dataset particularly important for both present and future comparative work. The dataset included four years of data on births (N=39) and copulations (N=170) for woolly monkeys, 10 years of data on births (N=35) and copulations (N=74) for spider monkeys, and seven years of data on fruit phenology.

Following the pattern seen in most atelins, the reproductive events of woolly monkeys and spider monkeys at TBS were distinctly seasonal. Births were concentrated between May and September, a time when ripe fruit was relatively scarce, while inferred conceptions occurred between September and January, when ripe fruit availability was increasing and then maintained at a high level. Although copulations were observed year-round, an overwhelming majority (>90% for *Lagothrix* and >80% for *Ateles*) took place between August and February, and most conceptions took place during this time period as well. After giving birth, woolly monkey females (N=9) took an average of ~20.1 months to resume copulating, while spider monkey females (N=8) took an average of ~29.5 months. In woolly monkeys, females that gave birth to males had significantly longer periods of postpartum sexual inactivity compared to those who gave birth to female infants, perhaps reflecting sex-biased investment in male offspring or greater metabolic demands associated with raising males. Once they resumed sexual activity post-partum, woolly monkey females took, on average, over six months to conceive, and spider monkey females, on average, took nearly eight months. The relatively narrow conception window for both species, coupled with long interbirth intervals (~ 3 years), reinforce the concept that mating opportunities – particularly those that lead to successful conception – are a limited resource. This situation may lead to behavioral strategies among animals of both sexes aimed at improve mating success and the likelihood of conception, e.g., active solicitation of males and polyandrous mating by females, female harassment of the copulations of competitors, large testes size in males, and elaboration of possible phenotypic markers of male quality.

With their large body size and "slow" life histories, atelins are generally thought to follow a "capital" breeding strategy, in which females do not conceive until they accumulate sufficient energy reserves for future reproductive events such as gestation and lactation (Nishimura 2003; Strier 1996; Strier and Ziegler 1997; Strier et al 2003). The data presented in Chapter 2, in conjunction with previous reports on atelin reproductive patterns, seem to corroborate the notion that atelins follow a capital breeding strategy with reproduction likely dependent on maternal body condition. However, there are important limitations to our study that prevent us from fully ruling out the idea that the woolly monkeys and spider monkeys are instead following a "relaxed income" breeding strategy. For example, we were not able to include data on weaning or lactation effort, which are key variables used to understand how females may time reproductive events in relation to food availability. Furthermore, we lacked direct measures of female body condition and hormonal profiles that would allow us to better evaluate when females are capable of conception. Given that repeated capture of adult female woolly monkeys to monitor physiology is both impractical and ethically suspect, more regular use of noninvasive techniques for tracking female body condition, reproductive function, and fecundity over time (e.g., photogrammetry, collecting fecal samples to assay progesterone to determine a female's reproductive state, or collecting urine to assay c-peptide – a direct measure of insulin production and thus of energy balance – to detect changes in a female's body condition) would be very valuable.

In **Chapter 3**, I examined the fission-fusion dynamics and ranging patterns of four social groups of woolly monkeys in relation to both fruit availability and mating opportunities. The dispersed nature of woolly monkey groups as they perform their daily activities has made it difficult for previous studies to quantitatively describe how spatial cohesion and ranging dynamics, both within and between groups, vary over time and in relation to temporal fluctuations in ecological and social resources, such as ripe fruit or mating partners. This study was unique in that multiple observers collected ranging and spatial association data simultaneously on individually recognized woolly monkeys, providing more precise measures of association, spatial cohesion, and space use than have been previously possible.

The woolly monkeys at TBS demonstrated relatively high degrees of fission-fusion dynamics, with groups subdividing frequently and showing temporally variable cohesion among group members. Importantly, the fission-fusion dynamics of woolly monkeys observed here differ both qualitatively and quantitatively from species with classically described "fission-fusion" patterns. That is, instead of the "individualistic" form of fission-fusion dynamics observed in spider monkeys and chimpanzees, or the predictable, "molecular" subgrouping patterns observed in multilevel societies of various cercopithecines (e.g., geladas and hamadryas baboons), the fission-fusion dynamics of woolly monkeys appear rather different. Although individuals did travel alone on occasion, it was much more common to find them in association with others, and fissions and fusions often involved sets of associating individuals rather than single animals. These sets, however, were not consistent and predictable as is observed in the grouping dynamics of multilevel societies (see Chapter 4), indicating that subgroup membership was flexible. Moreover, while it is rare to see all group members together among chimpanzees and spider monkeys except under specific circumstances (e.g., for limited periods of time during visitations to mineral licks: Link et al.), such a situation is not uncommon among woolly monkeys. All group members of the two smaller social groups (C and D) were found traveling as a cohesive unit in roughly 40% of party composition records. Larger groups (G and P), on the other hand, subgrouped more and were only found ranging as a cohesive unit in roughly 15% of party composition records, which is still far more often than is seen in spider monkeys or chimpanzees. Interestingly, when social groups were fissioned, subgroup size was found to be similar among the four social groups (median subgroup size: 7-8 adults and subadults). Compared to other atelin taxa that show higher degrees of fission-fusion dynamics (*Ateles*, some populations of *Brachyteles*), the subgroup size seen in *Lagothrix* is relatively high (*Ateles*: average subgroup size 3-8 individuals; *Brachyteles*: 2-5 individuals; reviewed in Baden et al. 2016). However when compared to other haplorrhine taxa we find that subgroup sizes are similar to those seen in several populations of chimpanzees and bonobos.

In contrast to the condition observed in chimpanzees and spider monkeys – where interactions among individuals from different social groups are almost always agonistic or hostile – woolly monkey party composition was not always limited to members of a single social group, and tolerant associations between members of some neighboring social groups occurred with relatively high frequency. In this study, most of the intergroup encounters observed occurred between groups C and G; 73% of these were considered to be either "affiliative" or "tolerant," and only 10% involved any direct forms of agonism (e.g., chasing). These two groups also shared the highest degree of home range overlap with one another, and parties composed of one or more individuals from both of these groups were common. Previous observers have suggested that these two social groups may have once been a single group that split sometime before 2006 (Schmitt 2010). Similar observations of relatively high occurrences of intergroup association have been commented on by Nishimura (1990), who much difficulty telling two social groups apart early in his observations, and it was not until he was able to recognize animals individually that he realized that what he thought was one social group was really two groups with tolerant intergroup associations.

As observed in other woolly monkey populations, home range overlap between neighboring groups in this study was extensive, with particular pairs of groups showing higher degrees of overlap than others. Although woolly monkeys are considered non-territorial, the four focal social groups I observed retained some exclusivity of their core areas, as evidenced by minimal core area overlap during most months of sampling for most pairs of groups.

Surprisingly, habitat-wide estimates of fruit availability had little to no influence on the observed variation in group cohesion and ranging patterns among the four groups, while an index of potential mating opportunities for males that I used did, suggesting that grouping and ranging dynamics in woolly monkeys may not primarily be the result of competition over food, but rather of competition and conflict over mating opportunities. This finding corroborates the importance of incorporating mating opportunities (and potentially female reproductive state) into models of fission-fusion behavior. However, it is worth noting that, because I only used habitat-wide estimates of ripe fruit availability and not any behavioral indicators of fruit consumption (e.g., time spent feeding on ripe fruit), the effects of fruit availability on range use and association patterns needs to be evaluated further.

In **Chapter 4,** I provide one of the most comprehensive and quantitative examinations of woolly monkey social structure yet, taking into account both patterns of spatial association as well as patterns of genetic relatedness among individuals within and between multiple social groups. More specifically, I applied social network analysis (SNA) to examine spatial association patterns and the emergent social structure of >50 individually recognized adult and subadult woolly monkeys from four well-known social groups (C, D, G, and P). In addition to SNA, I was able to successfully genotype 86 different individuals from the TBS population using 12 polymorphic microstallite loci. In tandem, these data helped elucidate the social and genetic complexity of woolly monkey society.

First, using hierarchical cluster analysis and measures of network modularity, I was able to confidently determine that the social interactions and spatial associations for most animals in our study population revolved around a consistent core group of individuals (i.e., the social group). Although individuals occasionally interacted with others from outside of their own social group for extended periods of time (and do so far more often than in many other species of anthropoid), the strength of these intergroup associations were significantly weaker than any association calculated between individuals from the same social unit. Furthermore, the four social groups delineated through SNA were the same social units acknowledged *a priori* by researchers at the site, demonstrating that woolly monkey social groups are entities that are readily recognizable in a manner that is both qualitative and quantitative.

Second, despite the seemingly "molecular" fission-fusion patterns exhibited by woolly monkeys, where subgroup composition and fission-fusion events were often marked by the association, or coming and going, of several individuals simultaneously rather than one individual at a time (detailed in chapter 3), we found little evidence that the composition of such subgroups, or subunits, were consistent over time. Instead, associations among woolly monkeys from the same social group proved to be fairly labile, and no significant differences in the strength of associations among subsets of animals from the same social group could be detected using party composition records. The lack of consistent substructure below the level of the social group deviates considerably from what is observed in most so-called "multilevel" societies that comprise several distinct social tiers. For example, in geladas, hamadryas baboons, and African elephants, individuals that belong to the same fundamental social unit (e.g., one-male units or family units) are so tightly associated that any individual selected can be used to represent that social unit at higher levels (de Silva and Wittemyer 2012). A randomly selected woolly monkey, however, cannot be used to represent an entire basal social unit in this same way. Thus, woolly monkey societies may be considered multilevel only in the sense that individuals differentially associate with more than one set of companions (de Silva and Wittemyer 2012) within and between social groups, but they are not necessarily multitiered, i.e., social units are not clearly defined below the level of social group, nor do they nest neatly within one another.

Third, although there were no clear subdivisions within woolly monkey social groups based on party composition records, individuals still appeared to exercise some selectivity of their association partners at close spatial proximity (<5 m), either through active coordination, i.e., seeking out and maintaining spatial proximity to preferred individuals, or by simply tolerating spatial proximity to some individuals more so than others. Across networks, the highest rates of association were found either between adults and their same-sex offspring or between a select few pairs of non-related opposite-sexed adults. These latter dyads most often comprised single males each associating predominantly with a particular receptive and reproductively active female during the mating season in 2014 and then continuing to maintain a high degree of spatial proximity with that female post-parturition in 2015. This pattern of association between particular males and particular females with young infants is consistent with the male reproductive strategy of “mate-then-care”, wherein males are more likely to associate with females that they have previously copulated with and thus have a greater chance of being the sire of that infant, rather than the strategy of “care-then-mate”, where males are thought to show considerable interest in a female and her infant to improve, or secure, reproductive opportunities with that female in the future (Kerhoas et al. 2016; Langergraber et al. 2013; Ménard et al. 2001; Ostner et al. 2013; Palombit et al. 1997; Smuts 1985). Still, more detailed data on male-female interactions, as well as on male-infant interactions, across both the mating and birthing seasons, combined with molecular analyses of paternity, are necessary to determine which of these male reproductive strategies is representative of woolly monkeys more broadly.

Finally, this study also provides ample behavioral and molecular evidence to demonstrate that, along with females, some male woolly monkeys also disperse from their natal group. Such a pattern is different from that seen in other atelins primate, which are characterized by routine male philopatry and almost obligate female dispersal (Di Fiore et al. 2011). Furthermore, through comprehensive genetic sampling of individuals in this population, we were able to corroborate previous findings that adult woolly monkeys of both sexes tend to have close same- and opposite-sexed genetic relatives (e.g., parent-offspring, siblings, half-siblings) residing both within and between adjacent social groups (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). How this extensive network of kin develops is not known precisely, but several possibilities emerge. First, given that adult males often retain a greater proportion of close adult kin, not only within their current social group but also across adjacent social groups, males that choose to leave their natal group may limit locational costs by practicing a “stepping-stone” model of dispersal (Kimura and Weiss 1964), transferring directly into neighboring groups (Isbell and van Vuren 1996). As observed in other primates with bisexual dispersal (e.g., red howler monkeys; Pope 1992), woolly monkey females appear to move much farther away from their natal group than males (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). Second, the extensive home range overlap and frequent intergroup encounters experienced by some pairs of groups may eventually facilitate dispersal between them through increased social knowledge of potential mating partners or the presence/absence of genetic relatives. Prolonged intergroup encounters, especially those formed between subsets of individuals from neighboring social groups, may also promote extragroup copulations. Indeed, if males that participate in extragroup copulations sire enough offspring, we could end up overestimating rates of dispersal by males even if all males actually stay in their natal group through adulthood (Di Fiore et al. 2009). Finally, behavioral observations as well as genetic 'recapture' data suggest that some individuals may move between social groups more than once, and for some females this secondary dispersal may occur even after successfully breeding in the prior social group (Di Fiore et al. 2009; Nishimura 2003; unpublished data). If secondary dispersal by adult females with dependents occurs frequently, patterns of paternity and male philopatry may be obfuscated even further. While our genetic dataset is a good step in understanding the kinship relationships among individuals within the four focal social groups, greater sampling effort is needed outside of these four groups. Furthermore, the genetic data used here simply provide a snapshot into the life of these long-lived animals, and more longitudinal sampling through behavioral observations of recognized individuals well, in addition to further genetic resampling, is needed to better understand not only the factors influencing an animal's decision to stay or disperse from their natal group, but what also attracts them to a new social group.

In sum, only through the concerted effort of multiple observers following individually recognized woolly monkeys simultaneously have we been able to start building a more robust, quantitative description of woolly monkey grouping dynamics. From these data a complex picture of woolly monkey society emerges, one characterized by a) flexibility in spatiotemporal association patterns not only among individuals from the same social group but also among those from different groups, b) ranging patterns that demonstrate high degrees of home range overlap among adjacent groups and shared space use that potentially facilitates intergroup interactions, and c) bisexual dispersal, where some males may stay in their natal group while others leave. As previously noted, such behavioral flexibility may indeed be a key evolutionary adaptation characterizing the entire atelin clade (Di Fiore and Strier 2004). Finally, this study raises the possibility that some of the social interactions within social groups (i.e., subgroup formation and preferred association partners) may be driven by competition over access to mates rather than competition over food resources. Given that mating and conception occur seasonally, and given that female woolly monkeys have relatively long interbirth intervals, reproductive opportunities may be viewed by both parties as a relatively limited resource.

Limitations and Future Directions

While the data presented here provide a robust assessment of woolly monkey ranging patterns, grouping dynamics, kinship, and reproductive seasonality that corroborates and extends earlier observations, there are several important limitations to our dataset that should be addressed and potentially rectified in future studies.

First, although this study was one of the first to actively monitor spatial cohesion among individually recognized woolly monkeys using multiple simultaneous observers, we could not always record the entire suite of social interactions that occurred during a full-day follow. For example, if two researchers were following the same social group, but that group then fissioned into three subgroups, we would only be able to collect data for the one or two distinct subgroups that our focal individuals were then a part of, losing information on association patterns among the individuals in that third subgroup, on where they traveled, and on whether they interacted with individuals from other social groups. Although we attempted to mitigate these issues by trying to evenly sample across our set of focal animals, certain individuals, particularly those in larger social groups, were just simply more difficult to locate than others. Furthermore, despite our best attempts to identify all of the individuals present in the same party simultaneously, as well as when they arrived or departed from that party, the size and dispersed nature of woolly monkey associations made this task quite challenging at times, and we acknowledge that as a result some individuals were likely excluded from party composition records.

To ensure a better characterization of the fission-fusion dynamics exhibited by woolly monkeys, one might try to increase the number of observers conducting simultaneous follows of monkeys in both the same and different social groups. Still, this solution may not be feasible in the long-term due to financial obligations and overall logistics of keeping researchers in the field for extended periods of time. An alternative solution to the challenge of more completely monitoring of the ranging and association patterns amongst woolly monkeys may be found through the use of Global Positioning Systems (GPS) and satellite tracking. Although all researchers were equipped with a handheld GPS while conducting behavioral follows, we could not always follow the same path our focal animals took while traveling from place to place, namely because our subjects were often traveling arboreally through an interconnected canopy while we were trying to navigate the hilly and sometimes inundated terrain below. Furthermore, because our behavioral sampling protocol called for us to follow a rotating schedule among different social groups, we were unable to continuously monitor how individuals were using their home ranges over extended periods of time and thus may have missed valuable information on how animals from different social groups coordinate their movements to either engage in or avoid intergroup encounters. Given that GPS technologies have dramatically improved over the last decade – smaller and lighter units, with longer battery life, that are capable of collecting fixes faster and with greater precision (Kays et al. 2015) – outfitting several woolly monkeys in each social group with GPS collars is becoming more practical and more appealing in terms of cost benefit trade-offs. Synchronously tracking the precise movements of multiple woolly monkeys from different social groups on a fine temporal scale should help to further refine our understanding of flexibility in the association patterns of animals both within and between neighboring social groups and allow us to ask more detailed questions – e.g., How often do individuals visit and return to important feeding trees or sleeping sites? Who do they travel with and who do they avoid? Do some individuals prefer to use certain parts of their home range over others? Are there significant sex differences in ranging patterns and space use? Where, how often, and for how long do individuals from adjacent social group associate, and do we find evidence from movement path analysis that these associations are actively sought after or avoided?

Second, while the genetic dataset used in this study was quite comprehensive, covering nearly all currently residing adult and subadult animals from the four social groups, and while the overall conclusions that can be drawn from our genetic data corroborate the findings of previous research (e.g., dispersal by animals of both sexes, the existence of a dispersed network of kin: Di Fiore and Fleischer 2005; Di Fiore et al. 2009), many questions still remain regarding the mechanisms by which woolly monkey dispersal occurs and how those in turn affect the kin structure of the population at large. For example, just how common is male dispersal from the natal group? How often are infants sired by extragroup males? Are secondary transfers by females (with or without their dependent offspring) common? Do males also undergo secondary transfers? How prevalent is parallel dispersal? Are males more likely to exhibit parallel dispersal than females? As in all behavioral studies, to adequately answer these questions, more long-term demographic data, behavioral observations, and genetic capture-recapture data on individually recognized monkey are necessary to determine which factors influence an animals' decisions as to whether to stay or disperse and how those decisions then shape the social interactions both within and between different social groups. I look forward to continue collecting these data and working with these datasets to further elucidate the intricacies of woolly monkey social dynamics and patterns of genetic relatedness.

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