Home range size, daily path length, and territoriality in Phayre's leaf monkeys (*Trachypithecus phayrei)*

A Thesis Presented

by

Katherine Marie Carl

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Master of Arts

in

Anthropology

(Physical Anthropology)

Stony Brook University

August 2009

Stony Brook University
The Graduate School

Katherine Marie Carl

We, the thesis committee for the above candidate for the Master of Arts degree, hereby recommend acceptance of this thesis.

Andreas Koenig, Ph.D., Thesis Advisor
Associate Professor, Anthropology

Carola Borries, Ph.D., Member
Research Associate Professor, Anthropology

Diane M. Doran-Sheehy, Ph.D., Member
Professor and Chair, Anthropology

This thesis is accepted by the Graduate School

Lawrence Martin
Dean of the Graduate School

Abstract of the Thesis

Home range size, daily path length, and territoriality in Phayre's leaf monkeys (*Trachypithecus phayrei)*

by

Katherine Marie Carl

Master of Arts

in

Anthropology

Stony Brook University

2009

Food distribution, availability, and presence of other groups are important factors in determining home range size, daily path length (DPL) and the ability of groups to defend their home ranges from conspecific intruders. Due to the widespread availability of leafy plants, folivorous primates are not typically considered to have a diet that is "economically defensible," and are not expected to exhibit aggressive territorial behavior toward conspecific groups. Consequently, folivore home ranges often overlap extensively. This study uses ranging data from three groups of a colobine species (Phayre's leaf monkey) at the Phu Khieo Wildlife Sanctuary (PKWS) in Northern Thailand to examine home range defensibility, using both complete and seasonal data divisions (according to temperature, food availability and mating and birth seasons). Contrary to expectations, Phayre's leaf monkeys (*Trachypithecus phayrei*) exhibit territorial behavior and maintain group home ranges with little to no overlap. GPS data collected from 2004- 2006 were used to obtain home range areas and average DPLs in order to test and compare two different methods of determining home range defensibility. When home range defensibility was calculated using the first method, Mitani and Rodman's *D* index, no clear pattern of seasonality emerged and only the smallest of the three groups was considered being able to consistently defend its home range. When Lowen and Dunbar's *M* index was used to calculate defensibility, all three groups were capable of home range defense at all times. Hence, while the results of the *M*-index confirm that even folivorous primates might be capable of home range defense, it was impossible to determine what role, if any seasonality plays in home range defensibility. In order to relate these findings to existing literature on territoriality, defensibility and diet, I examined and discussed the current literature on the definition of territorial behavior, methods of examining defensibility and, in particular home range defensibility in other colobine species.

Table of Contents

List of Tables

Chapter 1

Chapter 2

List of Figures

Chapter 1

Acknowledgements

I am sincerely thankful to Andreas Koenig for all of his patience, guidance and assistance. This project could not have been completed without his feedback and advice. Many thanks as well to Carola Borries for her insights and training at PKWS. Thanks to Diane Doran-Sheehy for feedback on the original attempt and presentation of this project.

I also wish to thank Amnoi B. Amphon S. Araya Y., C. Borries, J. Burns, Chakrit T., A. Derby, V. Ethier, L. Gibson, C. Gilbert, K. Jenks, J. Kamilar, A. Koenig, S. Kropidlowski, E. Lloyd, G. Pages, G. Preece, S. Suarez, Sucharest D. P. Terranova, B. Wheeler, T. Whitty and Wichian N. for generously allowing the use of their ranging data, and B. Wheeler for the use of his table of territoriality in colobines. M. Sisk and C. Scarry were instrumental in providing assistance with the use of ArcView and the Animal Movement Extension. Data collection at PKWS was funded by NSF grants BCS 0215542. Permission for data collection was granted by the National Research Council of Thailand (NRCT); National Park, Wildlife and Plant Conservation Department (DNP); Stony Brook University's IACUC #s 20001121-20061120.

Finally, thank you to Miljan Plavsic, Catherine & Paul Green and Erica Alliston for their tireless support and encouragement.

Chapter 1: Ranging patterns, seasonality and group size in Phayre's leaf monkeys

ABSTRACT

This study examines the general patterns of home range and daily path length in three groups of Phayre's leaf monkeys (*Trachypithecus phayrei*) at Phu Khieo Wildlife Sanctuary (PKWS) in the Chaiyaphum province of Northern Thailand. This study was conducted in order to provide a basis for the understanding of the relationship between home range size, average daily path length, diet and seasonality. While home range area and average daily path length are usually calculated using all available data, I investigated the possibility that both home range area and average daily path length (DPL) vary according to seasonality. In addition, I examined the influence of group size and the number of adult males on home range size ? and DPL. Data were divided into three different types of seasons: Season 1 separated the data according to temperature and rainfall (cold and dry, or hot and humid). Season 2 divided the data into times of high and low food availability. Season 3 examines birth seasons versus mating seasons. ArcView was used to calculate 95% Kernels of home range areas (both seasonal and complete), while DPLs were calculated using MS Excel. While there is an overall correlation of home range size with group size, the number of males in the group also influenced home range size. When home range and DPL were calculated according to temperature and rainfall, groups had slightly larger range sizes during hot and humid seasons than during cold, dry periods. There was no significant difference in range area during periods of high and low food availability. There was also no significant difference in range size during birth and mating seasons. Although group size had a significant effect on home range area, it did not significantly affect average DPLs. DPLs were, however, significantly (if marginally) lower during cold, dry seasons and during periods of low food availability. Finally, average DPLs were also significantly longer during mating seasons than during birth seasons. While these findings supported prior research indicating that home range size is primarily a function of group size, and that average DPLs are independent of group size, they did not support food availability as an influence on DPL in folivorous species. While changes in rainfall and ambient temperatures exerted some influence on DPL, the marked difference in average DPLs between mating and birth season may provide an interesting basis for further research.

INTRODUCTION

The area over which an animal, or a group of animals, ranges is principally determined by the need to obtain sufficient resources for survival and reproduction. Important resources include, but are not limited to: adequate food supply (in terms of both quality and quantity), potential mates, safe sleeping sites, and access to water (Trivers 1972; Emlen and Oring 1977; Clutton-Brock 1977; Clutton-Brock & Harvey 1977; Grant et. al. 1992; Maher and Lott 1995). The most commonly used term for this area is the 'home range', which may be defined as "the area over which an animal normally travels in pursuit of its routine activities (Jewell 1966)." On a day-to-day basis, animals should be expected to travel the minimal amount per day necessary to gain adequate nutrition and benefits from their home range (Charnoy, 1976). These daily movements are generally termed "daily path length," or DPL, defined as the amount that a group or individual travels within a twenty-four hour period. In nonhuman primates the use of different areas of the home range may vary on a monthly, seasonal or yearly basis, according to such factors as temperature, rainfall or food abundance (Jewell 1966; Bartlett 2007; Buzzard 2007).

The distribution of food, predators, and possible mates in an environment also plays a critical role in the structure of different primate social organizations (Wrangham 1980; van Schaik 1989; Sterck *et al.*1997). These factors, in turn, may affect the degree of overlap between the home ranges of conspecific groups of primates, or conspecific individuals (Bates 1970; Mitani and Rodman 1979; Grant 1992; Fashing 2001a; Harris 2005).

Because nutritional intake is the primary determinant of female reproductive success in primates, and male reproductive success is dependent on the distribution and availability of (receptive) females, food distribution therefore is usually the main factor influencing home range sizes and overlap in group home ranges (Trivers 1972; Emlen and Oring 1977). Primate species fall mainly into one of two categories: frugivorous (more than 40% of the diet consists of fruit) or folivorous (although other diet types include insectivorous, herbivorous, omnivorous or even gramnivorous). Fruits, which are spatially and temporally distributed in patches throughout an environment, are encountered more rarely than leaves and are easier to monopolize by groups and individuals. Frugivores generally have larger average daily path lengths than folivores, as fruits are more easily digested and of a higher nutritional quality than leaves, but far less abundant (Clutton-Brock and Harvey 1977a; Raemaekers 1980; Isbell 1983; Bennett 1986; Garber 1993; Olupot et al 1997; Goldsmith 1999; Di Fiore 2003; Doran et al 2004; Buzzard 2006). As a result, strong linear dominance hierarchies among females often evolved in frugivorous species, in which stronger individuals or individuals with matrilineal support, gain priority of access to fruit trees (or patches) and higher reproductive success. As well as increased within-group, direct contest competition for these resources, between-group competition also occurs as groups engage in a concentrated effort to keep conspecific intruders out of home ranges and defend fruit patches. Hence, frugivorous primates are expected to be far more territorial than folivorous primates (Wrangham 1980; van Schaik 1989; Sterck *et al.*1997).

In contrast, the traditional view of leaves, and leafy plant availability, is that they are distributed evenly and abundantly throughout most environments. They contain far less nutritional value than fruits per unit, but are far more abundant, in space and in time. Thus, monopolization of food is nearly impossible, and the energy expenditure required to defend an area far outweighs potential nutritional gain. Indirect scramble competition, rather than direct contest competition is expected to ensue and dominance hierarchies among females, if they exist, should be weak. Likewise, between group competition is unusual and folivore group home ranges generally show extensive overlap.

Recently, however, several researchers have concluded that leaves may indeed be a limited resource and that leafy patches are depleteable (Ganas and Robbins 2005; Koenig 2002; Koenig et al. 1998; Snaith and Chapman 2005). Younger leaves are higher in nutrient value and lower in tannin content than older leaves, and are distributed patchily in space and time (Waterman and Kool, 1994). Evidence in support of this comes from data showing that certain folivorous primates increase their average daily path lengths in response to higher food availability, which would not be expected if leafy food patches were not subject to depletion (Ganas and Robbins 2005; Koenig 2002; Koenig et al. 1998). Furthermore, Koenig et al. (1998) demonstrated that significant phytochemical heterogeneity does exist between young and old leaves, providing an incentive for individuals and groups to compete for younger leaves as they are a higher quality resource.

While food and feeding ecology is generally accepted as the greatest factor in group distribution and home range size, primate ranges may also be constricted by other factors. The presence of roads, changes in terrain or the presence of predators may restrict group movement. Additionally, density of primate groups in an area may play a role in group overlap. As density increases and food availability decreases, territorial behavior may emerge (Waser 1976; Barret and Lowen 1998). In such circumstances, the issue also arises of whether species behave territorially and aggressively or, alternatively, practice avoidance of other groups (Waser 1976; Gibson and Koenig, in revision).

Other factors found to affect ranging behavior are ambient temperature and rainfall. While the effects of temperature on ranging have not been studied extensively, animals react to temperature differences by engaging in both physiological and behavioral (e.g. moving less) thermoregulation (Stelzner 1988, Bronkowski and Altmann 1996). In addition, rainfall may play an important role in how far a group ranges. Anthropoid primates have been found to restrict their movement during periods of heavy rainfall, and therefore average daily path lengths on dry days often exceed those of rainy days (Chivers 1967, Altmann and Altmann 1970; Raemaekers 1980; Goldsmith 1999). If seasons differ dramatically in the amount of rainfall or in temperature, distinct differences in average daily path length should result.

Lastly mating competition and risk of infanticide or group takeover may affect ranging behavior. During the mating season, males in a group may increase daily path length and patrol home range boundaries extensively in order to prevent conspecific intruders from mating with receptive females (Kitchen et al. 2004). Bartlett (2009) found that seasonal variations in daily path length (in response to the availability of preferred resources) have a significant effect on the ability of male gibbons to defend and patrol female home ranges. When young, unweaned offspring are in a group males may also show higher rates of vigilance to prevent infanticide in the event of a group takeover (Kitchen 2004). As stated above, folivorous primates are not expected to exhibit territorial behaviors, nor are they usually known to do so. However, certain species of folivorous colobine species have been found to exhibit such behavior and to maintain home ranges with little overlap. While territory defense is considered impossible and a useless expenditure of energy for such species, there are currently two different methods of calculating whether groups are capable of defending their home ranges and no consensus exists on what actually constitutes territorial behavior versus avoidance behavior (Waser 1976; Maher and Lott 1995; Gibson and Koenig in review). Therefore, this study aims to address territoriality and home range defense in one colobine species, and to relate those findings to primate defensibility in general, providing further insight into the interactions of feeding ecology, mate defense and seasonality with ranging patterns and defensibility.

This study consists of two parts, with the objective of examining ranging patterns and territoriality in an Asian colobine. Chapter 1 examines the general pattern of home range size and daily path length, and their relationship to seasonality, group size and habitat quality in *Trachypithecus phayrei* at the Phu Khieo Wildlife Sanctuary, Thailand. In order to examine these relationships, ranging data were collected for three *T. phayrei* groups from PKWS, designated as PA, PB and PS. While home range size rarely correlates with group size in folivorous primates; hence it may be dependent on another factor, such as habitat quality.

Although home range area sizes and average daily path lengths are typically calculated using all available data, home ranges may expand or contract in response to such factors as temperature and food availability, depending on how far they must range to satisfy energy requirements (or, to look at it slightly differently, the energetic costs of ranging over smaller versus larger areas). Another factor may be whether females within a group are receptive, and therefore subject to male attempts at copulation, or if the birth of infants restricts maternal (and in turn, group) range size or DPL. Knowing more about these patterns of range use and DPL may allow for greater insight into how ranges vary seasonally and, in turn, help to investigate seasonal differences in home range defensibility (see Chapter 2).

Hence, I will examine the following predictions regarding ranging patterns and defensibility in three *T. phayrei* groups with home ranges that show little to no overlap at the Phu Khieo Wildlife Sanctuary in Northern Thailand:

1) *T. phayrei* home range sizes and defensibility indices are impacted by both the number of males in a group, and the total number of individuals.
    - Groups with more individuals show both larger overall home range size and seasonal range use than smaller groups (i.e. PB, the largest group, has a larger HR than both PA and PS).
    - PA, the only multi-male group, has both a proportionally larger home range, as well as higher seasonal defensibility indices as the two one-male groups, PB and PS.
    - When group size is small or shrinks significantly over time, group range contracts in response. The smallest group PS should therefore maintain the smallest home range.

2) *T. phayrei* home range sizes and defensibility indices are impacted by temporal periods (e.g. months, seasons or even years) in which resources show variation in abundance or distribution. Thus, *T. phayrei* groups at PKWS may be less able to

defend larger ranges during certain periods of the year, meaning that the ability to defend an entire home range is temporally flexible.

- Group range sizes contract and defensibility indices rise during colder, drier months when the days are shorter and individuals tend to conserve energy by moving less.
- During periods of food scarcity, range sizes increase (groups must travel farther to find enough food) and defensibility indices decrease as groups are unable to both search for food and defend territories.
- During mating seasons, average daily path lengths increase and defensibility indices increase, as males spend more time patrolling home range boundaries in order to prevent conspecific males from copulating with group females.
- During birth seasons, group ranges shrink and defensibility indices rise, due to decreased mobility of females with newborns.

3) Lowen and Dunbar's (1994) *M* index results in higher defensibility indices and shows that *T. phayrei* groups can more consistently defend home ranges, as *M* takes into account detection distance at HR boundaries instead of merely accounting for how often boundaries are crossed.

METHODS

Field site and study species:

Data for this study were collected at the Phu Khieo Wildlife Sanctuary (hereafter abbreviated as PKWS), located in the Chaiyaphum province of Northeastern Thailand. The sanctuary covers an area of 1,573km^2 and is located at 16°05- 35'N latitude, and 101°20-55'E longitude, with elevations above sea level ranging from 300- 1,300m (Khon Kaen University and Phu Khieo Wildlife Sanctuary 1995; Koenig et al. 2004). Part of the Western Isaan Forest Complex (along with eight other wildlife sanctuaries and nations parks), PKWS is primarily composed of hill and dry evergreen forest, with patches of dry dipterocarp forest (Borries et al. 2002). A single paved road passes through the sanctuary, demarcating the southern edge of the study site (Gibson and Koenig in revision). Average temperatures at PKWS range from 17-25°C, and monthly rainfall ranges from 0- 275 mm. PKWS contains a high diversity of fauna, including several primate species. While *Trachypithecus phayrei crepusculus* is the most common primate species (1.1 to 3.4 groups/km^2), white-handed gibbons (*Hylobates lar)*, rhesus (*Macaca mulatta)*, Assamese (*M. assamensis*), stump-tailed (*M. arctoides*) and pig-tailed macaques (*M. nemestrina*), along with slow lorises (*Nycticebus coucang)* are also found (Borries et al. 2002; Hassel-Finnegan et al. 2008).

Trachypithecus phayrei (common name, Phayre's leaf monkey or Phayre's langur) is a highly folivorous colobine species, ranging in areas of Bangladesh, Burma, India, Thailand and Vietnam (Groves 2001). *T. phayrei* are very similar in behavior and appearance to *Trachypithecus obscurus*, the spectacled langur, and due to their disputed taxonomic status are sometimes classified as a subspecies instead of a distinct species (Davies and Oates 1994 *in* Borries et al. 2002; but see Roos 2004; Brandon-Jones et al. 2004). Phayre's leaf monkeys are found in both uni-male and multi-male groups, and are mildly sexually dimorphic, with females weighing about 6.3 kg and males about 7.9 kg (Gupta and Kumar 1994; Fleagle 1999). Group sizes range from 3-30 individuals, and home ranges have been suggested to be relatively small (Gupta 2002). Although female *T. phayrei* exhibit linear dominance hierarchies (and possibly an age-inversed hierarchy), they are not philopatric and often disperse to other groups during between group encounters (Borries et al. 2004; Koenig et al. 2004). Males exhibit affiliative behavior quite frequently associating with each other and occasionally caring for infants (Koenig et al. 2004a).

Koenig, Borries and other researchers at PKWS began habituating *Trachypithecus phayrei* groups in October 2000. Each group took approximately one year to habituate, and although the data included in this study are taken from three focal groups (PA, PB and PS), there are currently four habituated *T. phayrei* groups within the sanctuary. Groups (Table 1.1) consisted of one or more adult males and circa seven females, along with immature members (average 16.3 individuals) (Koenig et al. 2004b). PA was a multi-male group, and consisted of 16-22 members during the period of study. PB and PS were single-male groups. PB was by far the largest group (24-31 members from March 2004 to December 2006), while PS contained the fewest number of members (ranging from 9-16 individuals). Changes in demography throughout the study period are further addressed in the analyses.

Although inter-group encounters are rare in the study population, *T. phayrei* show little overlap in home ranges between groups and exhibit a wide range of territorial behaviors when inter-groups encounters occur, including vocalizations, displays, chases, and even aggressive physical contact (Gibson and Koenig in revision). While males are typically the chief participants in these behaviors, female dispersal takes place during inter-group encounters as well; the observed relative lack of aggressive female participation in territorial behaviors may also be due to the fact that females take longer to habituate than males, and may be more reluctant to descend to the ground in the presence of researchers. Males also emit a 'whoop' long call that may function both within and between groups to regulate spacing (Koenig and Borries, *pers. comm.*).

Data collection:

Ranging data for this study were collected from all-day follows, where GPS data points were taken at first contact with the group, and subsequent data points were taken every thirty minutes, on the hour and the half-hour. GPS points were taken at the approximate center of a group. Home ranges for each group were calculated from all available, sufficiently accurate data (GPS error below 10 m) for the study period of March 2004- December 2006. Day ranges were taken only from "full days", in which no more than three data points were missing per day (Tables 1.2-1.4 show the number of full days in each season). Due to changes in day length, the definition of "full day" varied throughout the year. From March to September of each year, the first data point in a full day could be taken no later than 6:30 and the last point no earlier than 18:00. During October to February, the first point must have been taken no later than 7:00 and the last point no earlier than 17:00. On average, each group was followed for ca. 5 days per month. However, due to a separate research project, group PB was followed more extensively throughout late 2005 and the majority of 2006, hence more data were available for PB than for PA or PS.

Data analysis home range size:

GPS data points taken during daily follows were transcribed into MS Excel and converted to UTM coordinates. I deleted any GPS point that was not accurate to, or within, 10 meters. If a GPS reading had not been obtained, but the location was noted relative to a trail, UTM coordinates were retrieved from the UTM database of all trails in the area (Koenig and Borries, unpublished data).

All available and sufficiently accurate data were used to calculate home range size. I first calculated overall home range size throughout the period of data collection including all data from March 2004 to December 2006, and then calculated home range for Seasons 1, 2, and 3 for each year. For PA, a total number of 5,312 points were available from which to calculate home range, 10,886 for PB, and 3,919 points for PS.

One difficulty that occurs when studying ranging patterns is finding the point at which the complete home range has been covered. In order to find this point in the *T. phayrei* groups at PKWS, I divided each group's home range into 100x100 meter cells. Using Excel, I constructed pivot tables for each month of the study period, and noted the amount of new area added (i.e., new cells filled) to a group's range during each successive month, until the complete home range for each group had been covered. This method results in an asymptotic curve as the total home range size is approached, indicating the rate at which a group reuses parts of its home range (Waser 1976; Buzzard 2007).

In addition, I not only calculated home ranges for each season on an individual basis for each year, but also grouped seasons together for the entire duration of this study in order to examine overall trends and to increase the number of days from which to obtain home ranges and DPLs for each season. For example, I calculated home ranges for lean periods individually for 2004, 2005 and 2006 and also calculated the collective home range for all lean periods from 2004-2006. I used the Animal Movement Extension to ArcView 3.2a to calculate 95% Kernels for both overall home range and seasonal home range use (Hooge and Eichenlaub, 2000).

Data analysis- daily path length:

To calculate daily path lengths, only ranging data from complete all day follows (see seasonal starting and ending times of follows in *Data collection* above), lacking no more than 3 data points were used. For PA, 3582 data points were available from all complete days, for PB 8,066 points were available, and for PS, there were 2,843 usable data points. I first calculated an average daily path length from all available data points spanning the entire data collection period, as well as on a yearly basis. I subsequently averaged daily path length data according to seasonality for each season included in the data.

For data analysis, GPS data points were first converted to UTM coordinates. I then calculated the distance between each successive UTM coordinate using the Pythagorean Theorem, in which the distance between two points is:

$$\text{distance} = \text{square root } [(x1-x2)^2 + (y1-y2)^2]$$

Daily path length was then calculated as a sum of accumulated distances from the 30 minute samples for a given day, and averaged for the period of time, or season subject to consideration.

For a more detailed explanation of seasonal divisions, see above. Season 1 referred to climate variability throughout the year, Season 2 divided times of food availability into "lean" and "lush" periods and Season 3 examined DPLs during "mating" and "birth" seasons (Tables 1.2-1.4). For each season I calculated average DPLs on both an individual yearly basis and overall for 2004-2006 (e.g. for Season 2, I calculated average DPLs for lush periods individually for 2004, 2005 and 2006, as well as an average DPL for all lush periods from 2004-2006.

Season 1:

The climate at PKWS varies throughout the year, but may be divided into two general seasons: 1) hot and humid, with substantial rainfall, or 2) cold and dry, with little rainfall (Table 1.5). *T. phayrei* group home ranges may contract in response to colder temperatures, due to the shorter length of days that generally occur at the same time as such temperatures and the increased loss of energy associated with extensive travel. Mean temperature from January 2004 - December 2006 was 21.41°C (95% CI= 20.86-21.96 °C). Average rainfall for PKWS was 86.75 mm per month (95% CI= 59.86-113.65 mm; Table 1.5). In order to differentiate between the hot, humid and cold, dry seasons, I placed all months with rainfall measuring less than 59.86 mm into the cold and dry category. Although temperatures did vary with the seasons, the range of variability was smaller and did not always coincide with rainfall changes, making divisions somewhat less clear. Hence, temperature was not used as the main criterion for differentiating between seasons. Thus, hot and humid seasons had a temperature range of 19.75-24.06°C, with a mean of 22.38°C, and rainfall ranging from 65.78- 241.12 mm with a mean of 134.38 mm. Cold and dry seasons had a temperature range of 16.56-23.32°C, with an average temperature of 19.58°C, and rainfall ranging from 0.00- 42.02 mm per month, with a mean of 10.73mm.

Season 2:

Temporal variations in food abundance, density and number of available edible species may affect where and how far *T. phayrei* groups range within PKWS (i.e. how much of the overall home range is in use or is selectively used). Phenology data (Koenig and Borries, unpublished data) for flowering, fruiting and leafy plants show that the months of April through August can be characterized as "lush" for all three years in this study, in which the percentage of trees bearing young and mature leaves and fruits peaks and food availability is high, while October through February are months of low food availability, i.e., lean season. March and September were not included in either season, because they did not clearly fit into either the lean or the lush categories.

Season 3:

Mating season and infant births are a third factor that could have a strong effect on the range of the three *T. phayrei* groups at PKWS. During a mating season all members in a group, and male individuals in particular, may expand their daily path lengths and patrol the boundaries of their home range more vigilantly, either to keep out conspecific intruders or looking to mate with females within the group, or in order to pursue females in order to copulate with them themselves. On the other hand during the birth season the presence of unweaned infants may restrict the movement of females, and in turn, lower the average daily path length of the entire group. However, a contrasting possibility associated with infant births is that the daily path length actually *increases*, as females range further to satisfy the increased nutritional needs associated with lactation.

RESULTS

Demography:

During the complete study period, PA gained 5 members (through infant births and immigration of juveniles and females) and one natal male matured (February 2006) so that there were three adult males in the group. PB added a total of 7 members to the group through infant births. PS also added 7 new members in total via infant births and the immigration of 2 adult females (see Table 1.1). While PA gained a third adult male through maturation in 2006, PB contained the greatest number of adult females (10-11 throughout the study period). PS always had the smallest number of members, compared to PA and PB, but the number of adults in PS was close to that of PA for 2004 and 2005 (although PA, of course, had more adult males).

Complete home ranges:

95% Kernels for the complete home range (i.e. using all data from March 2004-December 2006) are shown in Figure 1.1. PA had a total home range of 1.071 km^2 (107.117 ha.), PB's home range spanned an area of 0.942 km^2 (94.195 ha.), and PS had a home range area of 0.580 km^2 (57.983 ha.). Thus, while the smallest group did indeed have the smallest range, the other groups had home ranges of similar size. On the other hand, the only multimale group (PA) had the largest home range.

Figure 1.2 depicts the home range asymptote for all three groups. The complete home range area for PA was not found until 8 December, 2006, the last day of data collection (238 days). PB's complete home range was obtained on 21October, 2006 (444/ 468 days of data collection), and PS's complete home range was found on 15 October, 2006 (162/172 days of data collection).

Yearly and seasonal ranges:

Table 1.6 shows home ranges in square kilometers and hectares for PA, PB and PS on a yearly basis, and expressed as a total percentage of the complete home range. Figure 1.3 shows 95% Kernels of each home range on a yearly basis. Taking all data from March 2004- December 2006 into account, all three *T. phayrei* groups at PKWS expanded their ranges. PA's range expanded from 0.945 to 1.145 km^2 during the study period (+ 0.201 km^2 since December 2004 and +0.144 km^2 since December 2005). PB's range grew from 0.858 to 0.985 km^2 in the same period (+0.127 km^2 since December 2004 and + 0.004 km^2 since December 2005). Finally, PS's range expanded from 0.590 to 0.642 km^2 (+ .053 km^2 since December 2004 and + 0.024 km^2 since December 2005). There is an overall correlation of home range size with group size (Spearman's r_s=0.669, N=9, P<0.05, 2-tailed; Figure 1.4). In addition, the social organization of the groups seemed to be important as well. The range of the multimale group PA was always larger as the group ranges of the single male groups (Mann-Whitney U-test: U=2.0, N_{multi}=3, N_{single}=6, z_{adj}=1.807, P=0.071, 2-tailed).

Season 1:

Table 1.7 lists home ranges in square kilometers and hectares for PA, PB and PS for Season 1, and expressed as a total percentage of the complete home range. Figures

1.5 and 1.6 show 95% Kernels of seasonal range size for PA, PB and PS, when the data are divided into hot, humid and cold, dry seasons. There does not initially appear to be any clear relationship or consistent directional trend between temperature, rainfall and home range size. However, when actually tested home ranges during the dry and cold season cover on average 0.619 km^2 (SD = 0.291) and during the hot and humid season 0.849 km^2 (SD = 0.239); the difference is marginally significant (Mann-Whitney U-test: U=29.0, $N_{cold\&dry}$=12, $N_{hot\&humid}$=9, z_{adj}=-1.777, P=0.076, 2-tailed).

Season 2:

There also does not appear to be any consistent direction of range expansion or contraction relative to food abundance and quality (Figures 1.7 and 1.8; Table 1.8). While PS did show higher range areas in lush seasons than in lean seasons, PA and PB showed larger range sizes when all lean seasons were combined (versus combined lush seasons) and no discernable pattern when individual seasonal range was compared. Home ranges during the lean season cover on average 0.820 km^2 (SD = 0.260) and during the lush season, 0.840 km^2 (SD = 0.206); the difference is not significant (Mann-Whitney U-test: U=36.0, N_{lean}=9, N_{lush}=9, z_{adj}=0.397, P=0.691, 2-tailed).

Season 3:

When the study period was divided on the basis of mating and birth seasons for all three groups, both PA and PS showed lower overall home ranges during birth seasons than during mating seasons, but PB had an increased home range size during birth seasons (Figures 1.9, 1.10 and 1.11; Table 1.9). However, there was no consistent direction of increased seasonal range size during individual mating and birth seasons for any of the three groups. Overall, the home ranges during the mating season cover on average 0.826 km^2 (SD = 0.227) and 0.704 km^2 (SD = 0.257); the difference is not significant (Mann-Whitney U-test: U=31.0, N_{mating}=9, N_{birth}=10, z_{adj}=-1.143, P=0.253, 2-tailed).

Complete and seasonal daily path lengths:

Table 1.10 shows daily path lengths for all three groups on a complete, yearly and seasonal basis. While home range sizes increased for each year from 2004- 2006 (Table 1.6), DPLs did not increase correspondingly for any of the groups, and in the case of PB, yearly DPLs actually decreased as home range area increased. There was no correlation of DPL with group size (Spearman's r_s=0.360, N=9, P=0.342, 2-tailed).

For Season 1, however, all three groups appear to have lower average daily path lengths in cold dry seasons (mean=0.916 km ±0.107 SD) than in hot and humid seasons (mean=1.065 km ±0.083 SD; Mann-Whitney U-test: U=15.0, $N_{cold\&dry}$=12, $N_{hot\&humid}$=9, z_{adj}=-2.772, P<0.006, 2-tailed).

When seasons were calculated on the basis of leaf and flower availability, all three *T. phayrei* groups generally had greater average daily path lengths in lush seasons, than in lean seasons (with the exception of all three groups during the second lush season). Statistically, indeed, DPLs were only marginally shorter in the lean season seasons (mean=0.979 km ±0.098 SD) than in the lush seasons (mean=1.034 km ±0.098 SD); the difference was non-significant (Mann-Whitney U-test: U=15.0, N_{lean}=9, N_{lush}=9, z_{adj}=-2.772, P<0.006, 2-tailed).

Finally, while all three groups had higher DPLs during mating seasons when all mating data are combined, only PS showed consistently higher DPLs during individual mating seasons versus birth seasons. When tested overall, however, DPLs during the mating season are indeed significantly longer (mean=1.074 km ±0.069 SD) than in the birth season (mean=0.935 km ±0.131 SD; Mann-Whitney U-test: U=14.0, $N_{mating}=9$, $N_{birth}=10$, $z_{adj}=-2531$, $P<0.02$, 2-tailed)

DISCUSSION

Demography:

Trachypithecus phayrei social structure, like that of some other colobine species, is somewhat flexible (Fleagle 1999) and groups may contain one or more adult males. Of the three *T. phayrei* groups at PKWS, only PA is a multi-male group, while PB and PS each include a single adult male. It is important to note that the number of males in a group may play an important role in ranging patterns and avoidance of other groups. Koenig and Gibson (in revision) found that PA was the only group that did not show any marked preference for or avoidance of border areas, while both PB and PS avoided borders that were adjacent to neighboring groups. Therefore, group “strength,” as measured by the number of males contained within the group seems to be an important factor in between-group encounters (or avoidance thereof). However, regardless of group size, “strength” or the threat from neighboring groups, overlap zones of home ranges are commonly under-utilized by many primate species, which may also occur in *T. phayrei* at PKWS (Wrangham et al. 2007).

Simultaneous increases in range and population size for all three groups indicate a link between range size and total group size. PS, the smallest group, did indeed maintain the smallest range, while PA and PB, which are similar in group size, had roughly similar range sizes. However, PA gained the fewest new members, yet showed the greatest increase in overall range size. Although range size does correlate to group size, when seasonal ranges were examined, average DPLs did not appear to correlate with group size, and PS had roughly the same average DPL as PA and PB. Furthermore, although home range sizes increased from 2004- 2006 for all three groups, average yearly daily path lengths actually decreased (PA = - 0.029 km, PB = - 0.023 km, PS = - 0.016 km). This may indicate that as groups grew in size, they used each area of their range for a shorter period and circulated through their home ranges (and added additional area to their home ranges) more rapidly than before. Ultimately, unless habitat quality for all three groups also simultaneously improved to a large degree between March 2004 and December 2006, which is not the case, thereby necessitating a shorter daily path length to obtain adequate food intake, DPL and group size do not appear to be correlated.

Furthermore, defensibility of a home range does not appear to be solely driven by group size in *T. phayrei,* as increased home range size and decreased daily path length means a smaller index of defensibility. However, as found by Koenig and Gibson (in revision) group “strength” (and consequently avoidance or lack thereof of neighboring groups) may not be simply a measure of the number of group members, or even the number of adult individuals, but may instead be due to the number of adult males in the group. Hence, home range size may be primarily driven by, the number of males in the group and, second, by the overall number of individuals, leading to the ranking from largest to smallest in terms of range size of: 1) PA 2) PB and 3) PS. While this does not support my prediction that home range size is predominantly driven by group size, but it does support the prediction that the number of males in the group plays a significant role in range size. Moreover, PS does maintain a far smaller home range than PA and PB, which indicates that overall group size does have *some* impact on home range size.

Complete home ranges:

As discussed above, complete home range correlates with both group size and the number of adult males in the group. One potential explanation of why complete home ranges were not reached for all three groups until late 2006 is that home ranges for each group expanded every year from 2004-2006 (with the exception of PS in 2004), and that the 95% Kernel areas for each group are greater in 2006 than the overall 95% Kernel areas. However, as the asymptotic curve show, the majority of the home ranges for all three groups are covered in late 2004/ early 2005, showing that a fairly accurate idea of *T. phayrei* home ranges may be obtained after about one year of data collection.

Yearly and seasonal ranges:

Although my second prediction was correct in that temperature and rainfall did have an effect on range size, the direction of range expansion and contraction was actually the opposite of my prediction. Contrary to expectation, ranges were significantly, if marginally, larger during cold, dry seasons than during hot and humid seasons. Hence temperature and rainfall may play a significant part in how far groups range on a daily basis. There was not, however, any significant or directional expansion in home range according to food availability, contradicting my prediction that group ranges would expand in times of limited food availability in order to fulfill nutritional requirements. A potential explanation is that groups use alternative foraging strategies during periods of low food availability, in which they settle for fewer preferred, but more densely distributed foods (Di Fiore 2003a; Bartlett *in* Lappan and Whittaker 2009). Finally, range size does not significantly increase or decrease in response to mating or birth seasons. To conclude, range size appears to be fairly independent of seasonality, and is far more heavily influenced by group size and strength.

Daily path length:

While home range size does depend on the number of individuals and the number of adult males in the group , average daily path length does not correlate with either variable. Furthermore, although group average DPLs are marginally shorter during cold, dry seasons than during hot and humid seasons (contradicting my prediction), there is no statistically significant difference. Likewise, DPLs did not differ significantly during periods of lush or lean food availability. This contradicts my second prediction, in which I expected that groups would need to range farther during seasons of lean food availability in order to obtain sufficient food intake. A potential explanation (seen above for home range size as well) is that groups use alternative foraging strategies during differential availability of preferred foods. In the future, this may be confirmed by collecting data on seasonal consumption ratios of fruits, flowers and leaves throughout the year. Also, leaf availability varies less than that of fruit (Buzzard 2007). Hence, while the quantity of preferred foods may be higher during lush seasons, food abundance may not alter enough to have an effect on home range size.

Finally, although DPLs for individual seasons did not show any consistent directional difference (with the exception of PS), when the overall seasons were tested, DPLs during the mating season were indeed significantly longer than during birth seasons. This substantiates my second prediction, and offers evidence that males patrol group boundaries more thoroughly during mating periods when females are receptive.

Wider implications:

The findings from this study support previous findings that home range size is primarily a function of group size, and support Gibson and Koenig's (in revision) findings that the number of adult males in the group also plays a role in range size. In species that exhibit both single and multi-male groups (e.g. *Nasalis larvatus*), these findings may play a role in predicting how groups behave with respect to conspecifics, and whether they maintain smaller home ranges or practice avoidance behaviors to avoid between group conflicts, female dispersal during such conflicts or group takeovers. The question of whether temperature and rainfall have consistently significant effects on range size remains to be further investigated.

My conclusion that average daily path lengths were independent of group size is also consistent with prior research. However, contrary to the expectation that daily path lengths ought to increase in folivores if (young) leaves are a limited resource, DPLs did not increase in response to higher periods of food availability (Ganas and Robbins 2005; Koenig 2002; Koenig et al. 1998). Further study is also required to substantiate or disprove the status of young leave as a limited, patchily distributed resource at other study sites, for other folivorous species. The possibility that groups increase daily path lengths in response to the presence of receptive females within the group was substantiated though, and the possibilities of similar findings in further research is intriguing.

Table 1.1. Changes in group composition from the beginning to the end of the study. AM = adult male, AF = adult female, SA = subadult, J = juvenile, I = infant.

Group	Year	Month	Average day range [km]	N AM	N AF	N SA	N J	N I	Total	Changes in group composition
PA	2004	March	759.59	2	5	0	4	4	16	8 I born, 1 I disappeared, 6 I became J, 5 J immigrated into PA, 5 J disappeared, 2 J became SA, 5 SA became AF, 3 AF immigrated into PA, 4 AF disappeared, 1 SA became AM
PA	2006	December	1119.22	3	6	1	7	5	22	
PB	2004	March	785.58	1	12	0	0	11	24	12 I born, 2 I disappeared, 13 I became J, 2 J disappeared, 2 J became SA, 2 AF disappeared
PB	2006	December	915.96	1	10	2	9	9	31	
PS	2004	March	963.14	1	4	0	1	3	9	7 I born, 7 I became J, 1 J became SA, 2 AF immigrated into PA, 2J and 1 AF disappeared, 1 SA became AF
PS	2006	December	726.27	1	5	1	5	4	16	

Table 1.2. Number of total and full days of data included in each year or season for group PA

Subdivision	**Season**	**Year(s)**	**Month(s)**	**N days total**	**N complete days**
Complete	All	2004-2006	All	237	142
Year	2004	2004	All	80	44
	2005	2005	All	92	54
	2006	2006	All	65	44
Weather	All hot and humid	2004-2006	Various	163	95
	All cold and dry	2004-2006	Various	74	47
	Cold and dry	2004	March	5	1
	Hot and humid	2004	Apr-Sept	56	34
	Cold and dry	2004-05	Oct-Mar	41	26
	Hot and humid	2005	Apr-Nov	64	33
	Cold and dry	2005-06	Dec-Feb	17	10
	Hot and humid	2006	Mar-Oct	43	28
	Cold and dry	2006	Nov- Dec	11	10
Food availability	All lush	2004-2006	Apr- Aug	120	71
	All lean	2004-2006	Oct-Feb	75	48
	Lush	2004	Apr- Aug	49	29
	Lean	2004-05	Oct-Feb	31	18
	Lush	2005	Apr- Aug	44	25
	Lean	2005-06	Oct-Feb	27	16
	Lush	2006	Apr- Aug	27	17
	Lean	2006	Oct-Feb	17	14
Mating & birth	All mating	2004-2006	Various	161	96
	All birth	2004-2006	Various	76	46
	Birth (1)	2004	Mar	5	1
	Mating (1)	2004	Apr-Dec	75	43
	Birth (2)	2005	Jan-Aug	66	42
	Mating (2)	2005-06	Sept-Feb	37	18
	Birth (3)	2006	Mar	5	3
	Mating (3)	2006	Apr- Feb	49	35

Table 1.3. Number of total and full days of data included in each year or season for group PB.

Subdivision	Season	Year(s)	Month(s)	N days total	N complete days
Complete	All	2004-2006	All	468	314
Year	2004	2004	All	73	56
	2005	2005	All	144	81
	2006	2006	All	251	177
Weather	All hot and humid	2004-2006	Various	328	223
	All cold and dry	2004-2006	Various	140	91
	Cold and dry	2004	March	9	5
	Hot and humid	2004	Apr-Sept	42	35
	Cold and dry	2004-05	Oct-Mar	60	43
	Hot and humid	2005	Apr-Nov	91	43
	Cold and dry	2005-06	Dec-Feb	60	36
	Hot and humid	2006	Mar-Oct	195	145
	Cold and dry	2006	Nov- Dec	11	7
Food availability	All lush	2004-2006	Apr- Aug	236	161
	All lean	2004-2006	Oct-Feb	142	95
	Lush	2004	Apr- Aug	35	29
	Lean	2004-05	Oct-Feb	48	36
	Lush	2005	Apr- Aug	65	29
	Lean	2005-06	Oct-Feb	76	47
	Lush	2006	Apr- Aug	136	103
	Lean	2006	Oct-Feb	18	12
Mating & birth	All mating	2004-2006	Various	341	230
	All birth	2004-2006	Various	127	84
	Mating (1)	2004	Mar- Oct	57	45
	Birth (2)	2005	Nov- Mar	54	38
	Mating (2)	2005-06	Apr- Aug	65	29
	Birth (3)	2006	Sept- Jan	62	39
	Mating (3)	2006	Feb- Oct	219	156
	Birth (4)	2006	Nov- Dec	11	7

Table 1.4. Number of total and full days of data included in each year or season for group PS.

Subdivision	Season	Year(s)	Month(s)	N days total	N complete days
Complete	All	2004-2006	All	172	112
Year	2004	2004	All	59	48
	2005	2005	All	53	33
	2006	2006	All	60	31
Weather	All hot and humid	2004-2006	Various	110	62
	All cold and dry	2004-2006	Various	62	50
	Cold and dry	2004	March	10	8
	Hot and humid	2004	Apr-Sept	35	27
	Cold and dry	2004-05	Oct-Mar	27	23
	Hot and humid	2005	Apr-Nov	35	19
	Cold and dry	2005-06	Dec-Feb	15	10
	Hot and humid	2006	Mar-Oct	40	16
	Cold and dry	2006	Nov- Dec	10	9
Food availability	All lush	2004-2006	Apr- Aug	75	44
	All lean	2004-2006	Oct-Feb	63	47
	Lush	2004	Apr- Aug	30	25
	Lean	2004-05	Oct-Feb	23	20
	Lush	2005	Apr- Aug	20	10
	Lean	2005-06	Oct-Feb	25	15
	Lush	2006	Apr- Aug	25	9
	Lean	2006	Oct-Feb	15	12
Mating & birth	All mating	2004-2006	Various	63	37
	All birth	2004-2006	Various	109	75
	Birth (1)	2004	Mar-May	20	17
	Mating (1)	2004	Jun- Sept	25	18
	Birth (2)	2005	Oct- May	34	26
	Mating (2)	2005-06	Jun- Sept	18	11
	Birth (3)	2006	Oct- May	40	20
	Mating (3)	2006	Jun- Sept	20	8
	Birth (4)	2006	Oct- Dec	15	12

Table 1.5. Temperature and rainfall data and classification of weather seasons.

Year	Month	Average temperature [°C]	Rainfall [mm]	N days with rain	Season
All	All cold, dry seasons	19.58	10.732[a]	23	Cold, dry
All	All hot, humid seasons	22.38	134.38[a]	376	Hot, humid
2004	March	23.32	42.02	8	Cold, dry
2004	April	24.06	84.48	16	Hot, humid
2004	May	22.76	241.12	23	Hot, humid
2004	June	22.18	177.98	19	Hot, humid
2004	July	22.63	144.32	18	Hot, humid
2004	August	22.75	88.66	13	Hot, humid
2004	September	22.02	113.52	19	Hot, humid
2004	October	20.41	1.10	1	Cold, dry
2004	November	19.43	1.98	2	Cold, dry
2004	December	16.56	0.00	0	Cold, dry
2005	January	18.42	2.42	1	Cold, dry
2005	February	22.67	8.80	2	Cold, dry
2005	March	22.34	24.42	6	Cold, dry
2005	April	23.42	190.74	20	Hot, humid
2005	May	23.86	104.72	14	Hot, humid
2005	June	23.26	58.74	15	Hot, humid
2005	July	22.35	194.04	18	Hot, humid
2005	August	22.39	80.52	22	Hot, humid
2005	September	21.76	295.68	28	Hot, humid
2005	October	21.13	66.88	13	Hot, humid
2005	November	19.75	123.64	9	Hot, humid
2005	December	17.12	0.00	0	Cold, dry
2006	January	17.81	0.00	0	Cold, dry
2006	February	20.21	40.04	2	Cold, dry
2006	March	22.41	151.14	12	Hot, humid
2006	April	22.43	175.78	20	Hot, humid
2006	May	22.26	121.88	18	Hot, humid
2006	June	23.25	81.62	16	Hot, humid
2006	July	22.84	65.78	18	Hot, humid
2006	August	22.40	195.80	16	Hot, humid
2006	September	21.48	91.50	19	Hot, humid
2006	October	21.04	107.90	10	Hot, humid
2006	November	19.83	8.00	1	Cold, dry
2006	December	16.80	0.00	0	Cold, dry

[a] average monthly rainfall of all months within season

Table 1.6. Home ranges on a yearly basis, calculated for all three groups and shown in square kilometers, hectares, and as a percentage of the complete home range.

	PA			PB			PS		
Year	**km^2**	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**	**km^2**	**ha**	**% Tota l HR**
Complete HR	1.071	107.117	100	0.942	94.195	100	0.580	57.983	100
2004	0.945	94.456	88	0.858	85.799	91	0.590	58.968	102
2005	1.001	100.089	93	0.982	98.174	104	0.403	40.277	69
2006	1.145	114.534	107	0.985	98.529	105	0.642	64.226	111

Table 1.7. Home ranges for Season 1 for PA, PB and PS. HH = hot & humid; CD = cold & dry.

	PA			**PB**			**PS**		
	km^2	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**
Complete HR	1.071	107.117	100	0.942	94.195	100	0.580	57.983	100
All cold/ dry	0.964	96.432	90	0.954	95.356	101	0.519	51.879	89
All hot/ humid	1.083	108.323	101	1.038	103.835	110	0.630	63.025	109
CD 1	0.467	46.687	44	0.192	19.151	20	0.357	35.746	62
HH 1	0.742	74.245	69	0.950	95.018	101	0.572	57.1536	99
CD 2	0.701	70.073	65	0.845	84.469	90	0.488	48.759	84
HH 2	1.075	107.475	100	1.067	106.728	113	0.487	48.744	84
CD 3	0.664	66.438	62	1.111	111.065	118	0.331	33.143	57
HH 3	1.143	114.343	107	0.943	94.297	100	0.662	66.169	114
CD 4	0.981	98.073	92	0.895	89.519	95	0.398	39.843	69

Table 1.8. Home ranges for Season 2 for PA, PB and PS. LU = lush; LE = lean.

	PA			**PB**			**PS**		
	km^2	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**
Complete HR	1.071	107.117	100	0.942	94.195	100	0.580	57.983	100
All lush	1.063	106.251	99	0.977	97.732	104	0.657	65.705	113
All lean	1.117	111.708	104	1.113	111.272	118	0.624	62.391	108
LU 1	0.759	75.863	71	0.964	96.357	102	0.561	56.083	97
LE 1	0.821	82.115	77	0.922	92.152	98	0.550	54.971	95
LU 2	1.022	102.161	95	0.965	96.451	102	0.576	57.552	99
LE 2	0.942	94.239	88	1.135	113.505	120	0.413	41.310	71
LU 3	1.072	107.207	100	1.003	100.334	107	0.641	64.099	111
LE 3	0.981	98.073	92	1.083	108.282	115	0.529	52.889	91

Table 1.9. Home ranges for Season 3 for PA, PB and PS. B = birth; M = mating .

	PA			**PB**			**PS**		
	km^2	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**	**km^2**	**ha**	**% Total HR**
Complete HR	1.071	107.117	100	0.942	94.195	100	0.580	57.983	100
All mating	1.154	115.360	108	0.916	91.597	97	0.654	65.393	113
All birth	0.883	88.275	82	1.075	107.543	114	0.508	50.809	88
B 1	0.467	46.687	44				0.344	34.380	59
M 1	0.849	84.920	79	0.832	83.190	88	0.579	57.877	100
B 2	0.889	88.918	83	0.807	80.661	86	0.567	56.675	98
M 2	0.998	99.786	93	0.965	96.451	102	0.442	44.205	76
B 3	0.852	85.177	80	1.173	117.341	125	0.512	51.172	88
M 3	1.151	115.074	107	0.961	96.132	102	0.655	65.497	113
B 4				0.895	89.519	95	0.529	52.889	91

Table 1.10. Daily path lengths [km] for PA, PB and PS, shown for complete, yearly and seasonal time divisions, and with standard deviations (in kilometers). HH = hot & humid; CD = cold & dry; LU= lush; LE = lean; B = birth; M= mating.

Subdivision	**Season**	**PA**	**PA (sd)**	**PB**	**PB (sd)**	**PS**	**PS (sd)**
Complete	Complete HR	1.107	0.267	1.006	0.242	0.940	0.269
Year	2004	1.172	0.281	1.025	0.241	0.969	0.266
	2005	1.024	0.253	1.003	0.271	0.887	0.306
	2006	1.143	0.247	1.002	0.229	0.953	0.231
Weather	All HH	1.145	0.281	1.023	0.246	1.008	0.237
	All CD	1.030	0.219	0.966	0.239	0.855	0.285
	CD 1	0.728	0.000	0.833	0.292	0.963	0.369
	HH 1	1.225	0.275	1.084	0.234	0.999	0.219
	CD 2	1.026	0.233	0.968	0.267	0.836	0.313
	HH 2	1.034	0.269	1.027	0.272	0.993	0.278
	CD 3	1.068	0.232	1.003	0.191	0.835	0.237
	HH 3	1.178	0.270	1.006	0.233	1.043	0.224
	CD 4	1.033	0.170	0.860	0.223	0.833	0.183
Food availability	All LU	1.101	0.254	1.019	0.236	0.992	0.218
	All LE	1.082	0.232	0.987	0.250	0.876	0.256
	LU 1	1.184	0.204	1.050	0.239	1.022	0.209
	LE 1	1.040	0.210	0.940	0.272	0.866	0.270
	LU 2	0.989	0.270	0.997	0.265	0.837	0.175
	LE 2	1.094	0.231	1.028	0.223	0.917	0.288
	LU 3	1.127	0.261	1.016	0.229	1.081	0.220
	LE 3	1.122	0.267	0.963	0.274	0.843	0.200
Mating & birth	All M	1.152	0.261	1.015	0.237	1.046	0.230
	All B	1.011	0.257	0.983	0.254	0.888	0.273
	B1	0.728	0.000			0.962	0.275
	M1	1.183	0.277	1.052	0.244	1.018	0.238
	B2	1.004	0.256	0.958	0.276	0.825	0.296
	M2	1.116	0.228	0.997	0.265	1.021	0.262
	B3	1.203	0.199	1.028	0.231	0.934	0.274
	M3	1.134	0.260	1.008	0.230	1.141	0.148
	B4			0.860	0.223	0.843	0.200

Figure legends

Figure 1.1. Home range areas of the study groups (PA, PB, PS) for the entire period. 95% Kernels calculated from all available data. PA is shown in red, PB in blue and PS in yellow.

Figure 1.2. Cumulative home range size of the study groups (PA, PB, PS) for the entire period. PA is shown in red, PB in blue and PS in yellow. An individual plot measured 100 x 100 m.

Figure 1.3. Home range areas of the study groups (PA, PB, PS) over successive years. 95% Kernels for group home ranges on a yearly basis. PA is shown in red, PB in blue and PS in yellow.

Figure 1.4. Annual home range size (2004, 2005, 2006) of the study groups (PA, PB, PS) in relation to group size (all individuals including infants).

Figure 1.5. Home range areas of the study groups (PA, PB, PS) during the cold & dry and hot & humid season. 95% Kernels assembled from all data (2004-2006) according to temperature and rainfall data. PA is shown in red, PB in blue and PS in yellow.

Figure 1.6. Seasonal home range areas of the study groups (PA, PB, PS) during successive cold & dry and hot & humid seasons. Seasonal ranges (95% Kernels) according to temperature and rainfall. PA is shown in red, PB in blue and PS in yellow.

Figure 1.7. Home range areas of the study groups (PA, PB, PS) during the lean and the lush season. 95% Kernels assembled from all data (2004-2006) according to food availability. PA is shown in red, PB in blue and PS in yellow.

Figure 1.8. Seasonal home range areas of the study groups (PA, PB, PS) during successive lean and lush seasons. Seasonal ranges (95% Kernels) according to periods of food availability. PA is shown in red, PB in blue and PS in yellow.

Figure 1.9. Home range areas of the study groups (PA, PB, PS) during the mating and birth season. 95% Kernels assembled from all data (2004-2006) according to mating and birth seasons. PA is shown in red, PB in blue and PS in yellow.

Figure 1.10. Seasonal home range areas (95% Kernels) of the study groups (PA, PB, PS) during successive mating seasons. PA is shown in red, PB in blue and PS in yellow.

Figure 1.11. Seasonal home range areas (95% Kernels) of the study groups (PA, PB, PS) during successive birth seasons. PA is shown in red, PB in blue and PS in yellow.

Fig. 1.1

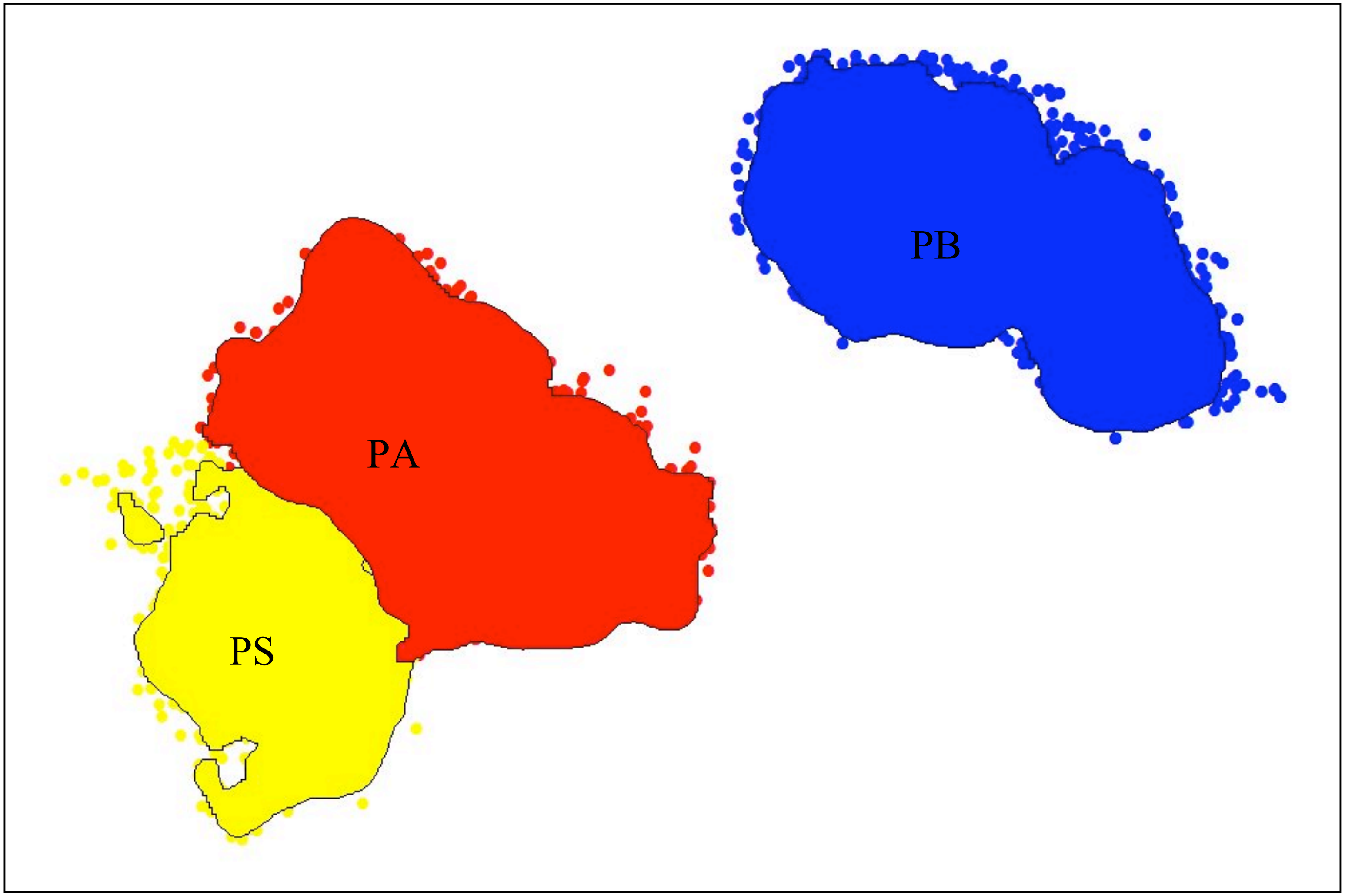


Fig. 1.2

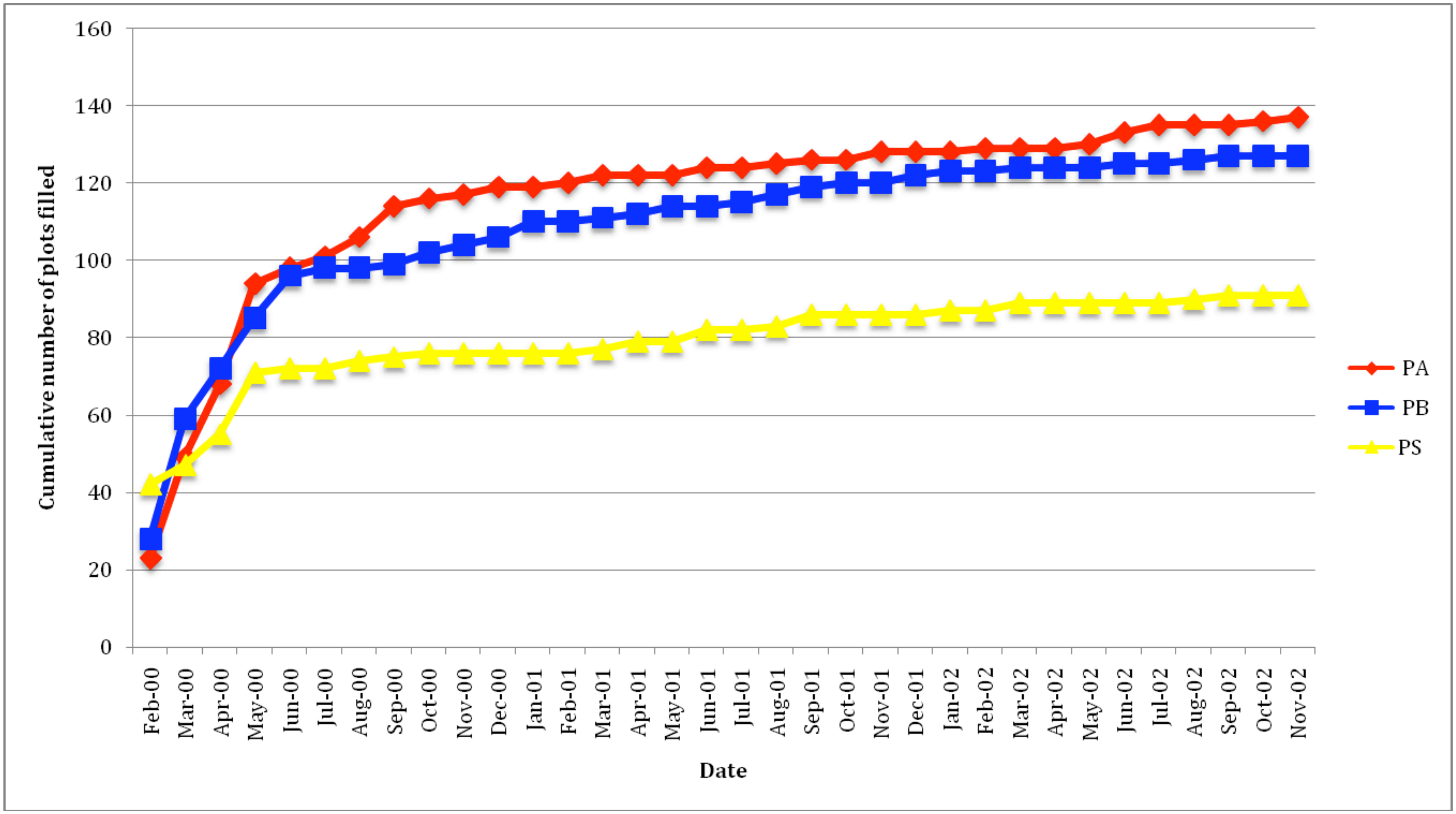
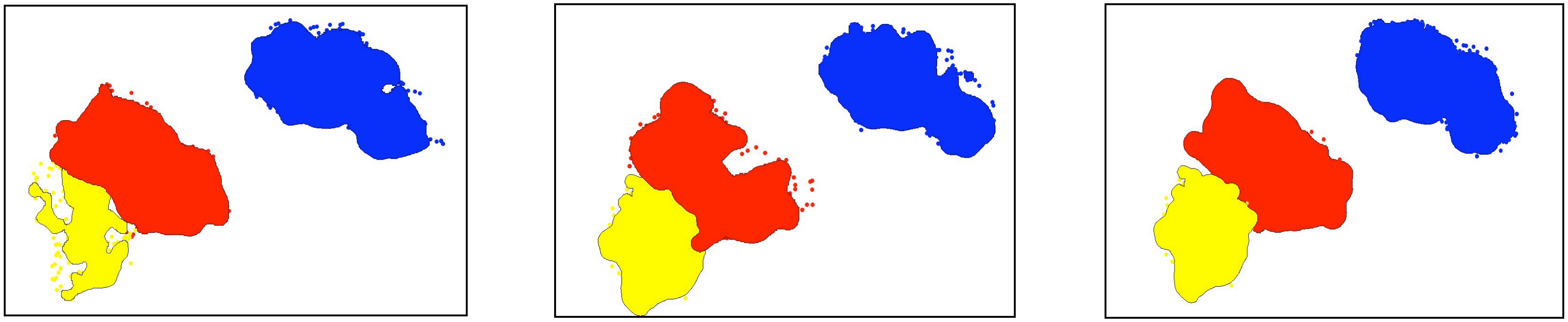

Cumulative number of plots filled
160
140
120
100
80
60
40
20
0
Feb-00
Mar-00
Apr-00
May-00
Jun-00
Jul-00
Aug-00
Sep-00
Oct-00
Nov-00
Dec-00
Jan-01
Feb-01
Mar-01
Apr-01
May-01
Jun-01
Jul-01
Aug-01
Sep-01
Oct-01
Nov-01
Dec-01
Jan-02
Feb-02
Mar-02
Apr-02
May-02
Jun-02
Jul-02
Aug-02
Sep-02
Oct-02
Nov-02
Date
PA
PB
PS

Fig. 1.3

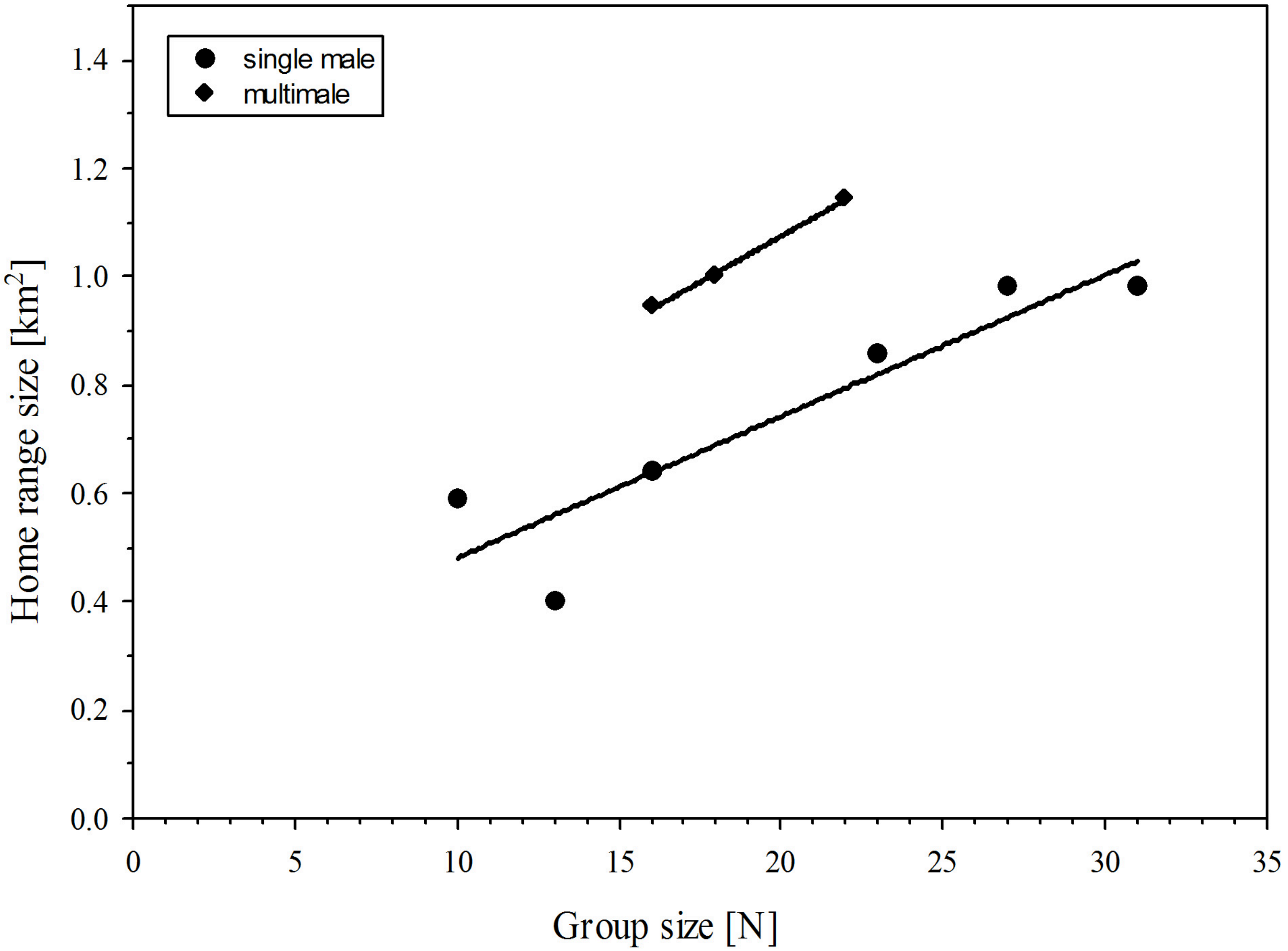


2004

2005

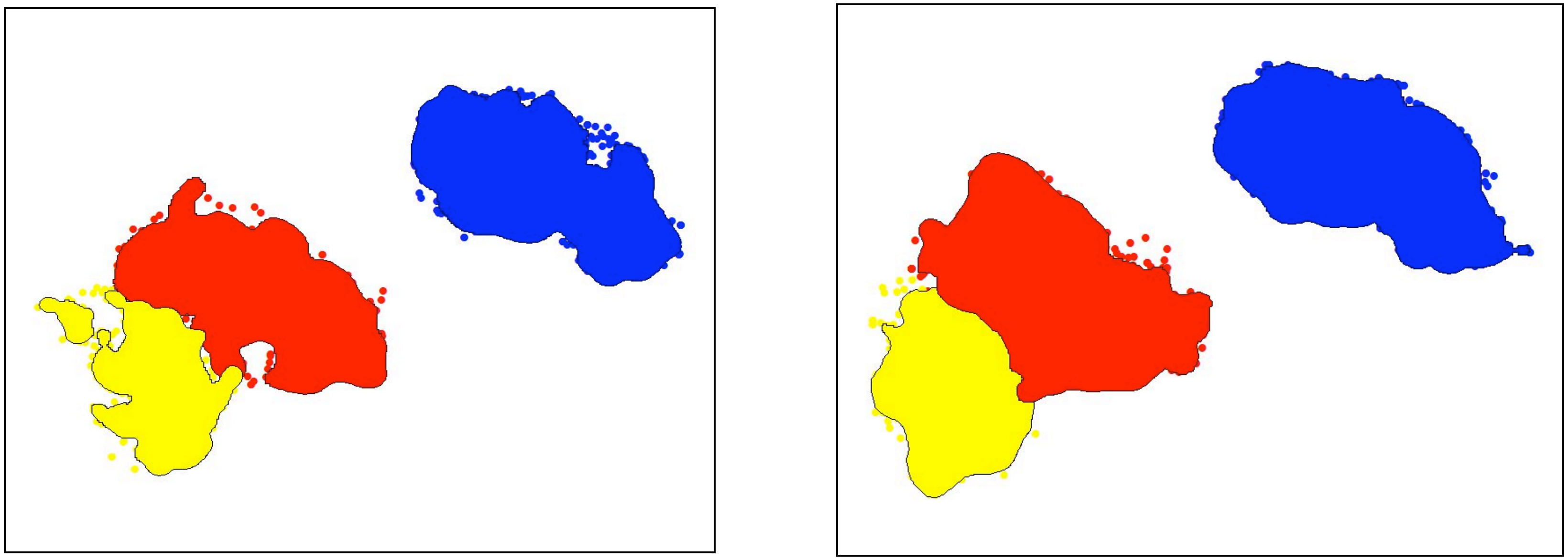
2006

Fig. 1.4



single male
multimale
Home range size [km^2]
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
Group size [N]

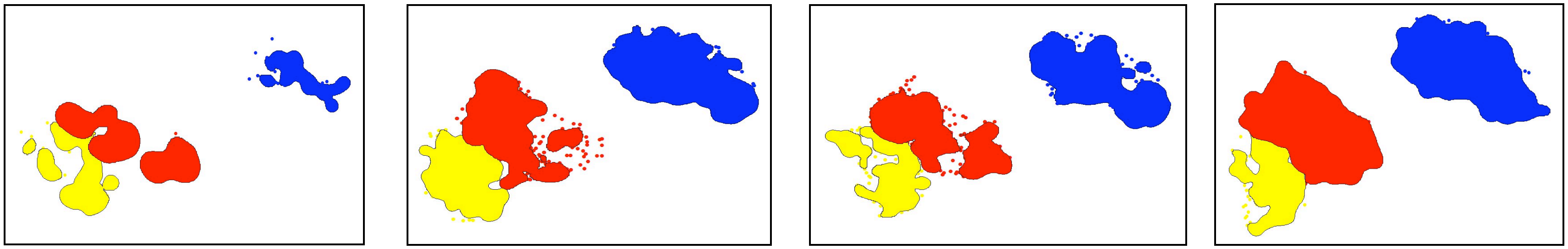
Fig. 1.5s



Cold and dry

Hot and humid

Fig. 1.6

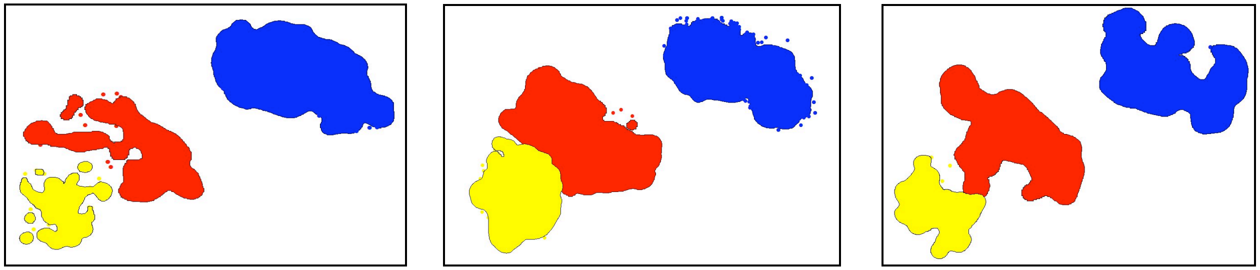


May 2004

April- September 2004

October 2004- March 2005

April- November 2005

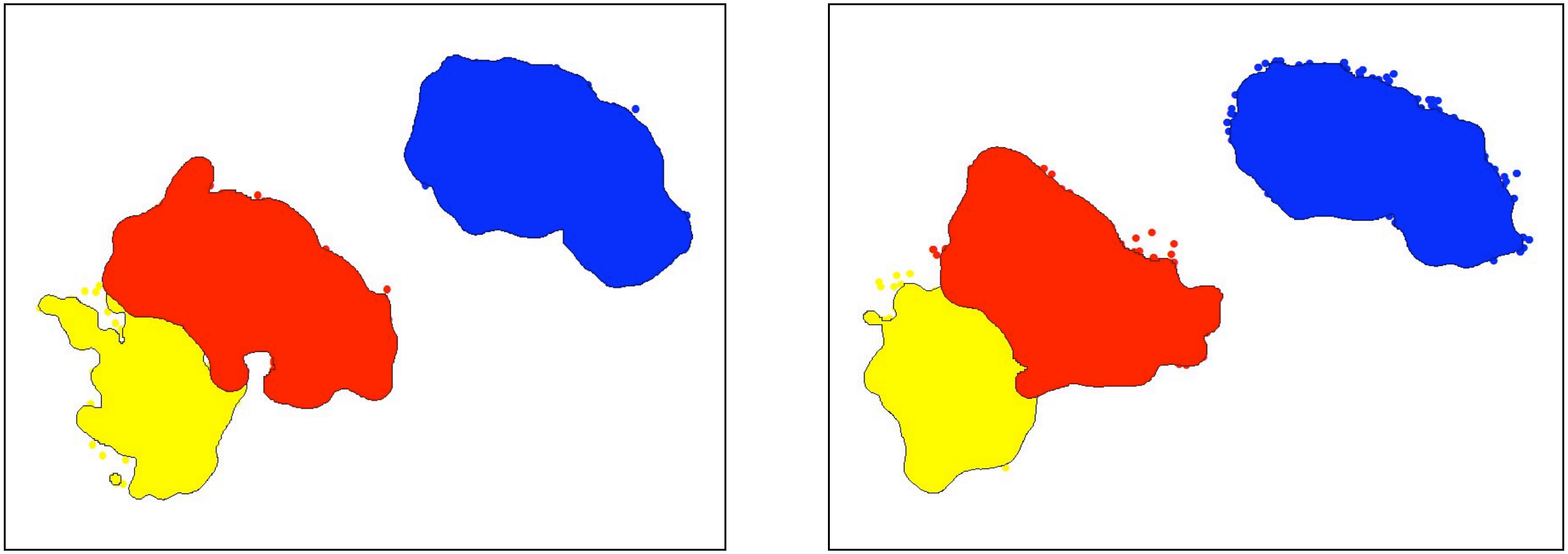


December 2005- February 2006

March- October 2006

November- December 2006

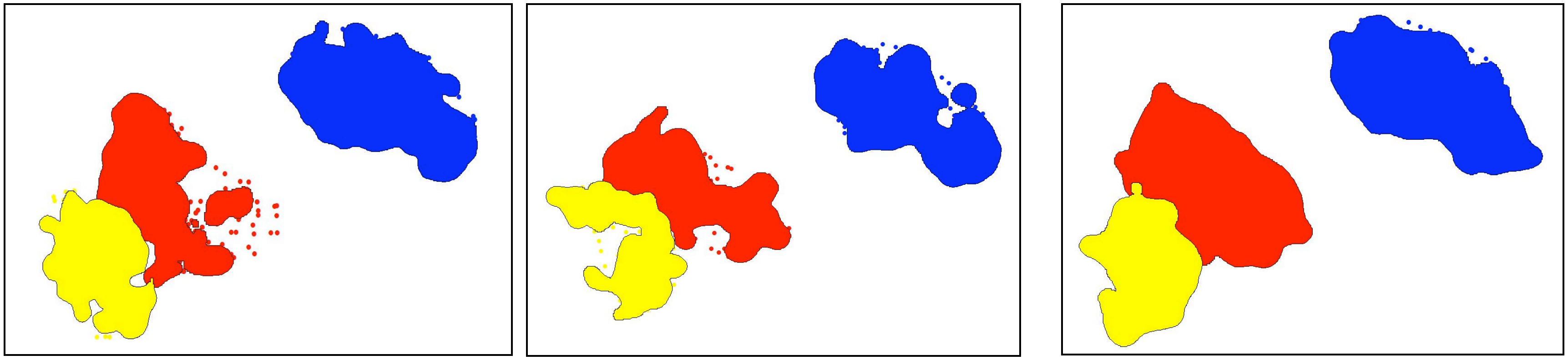
Fig. 1.7



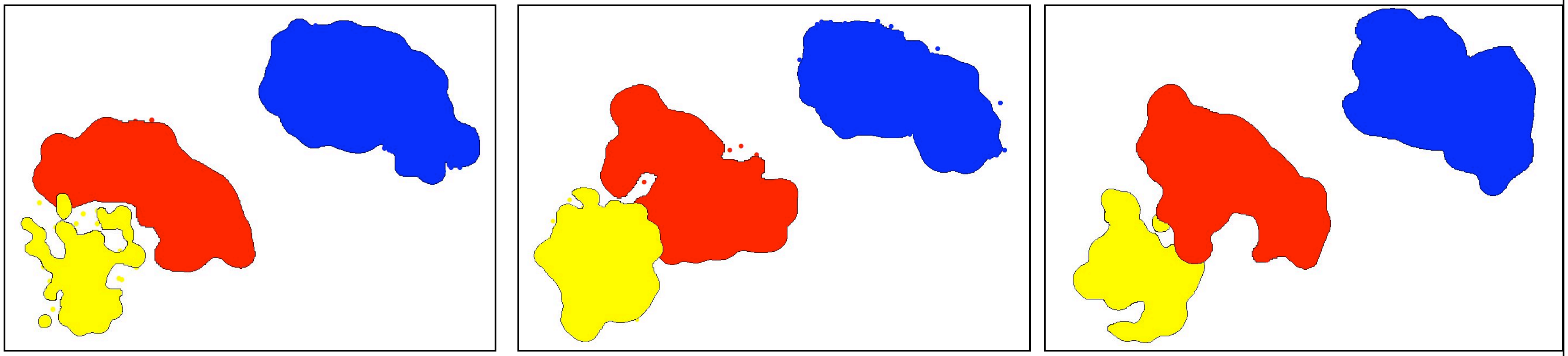
Lean season

Lush season

Fig. 1.8

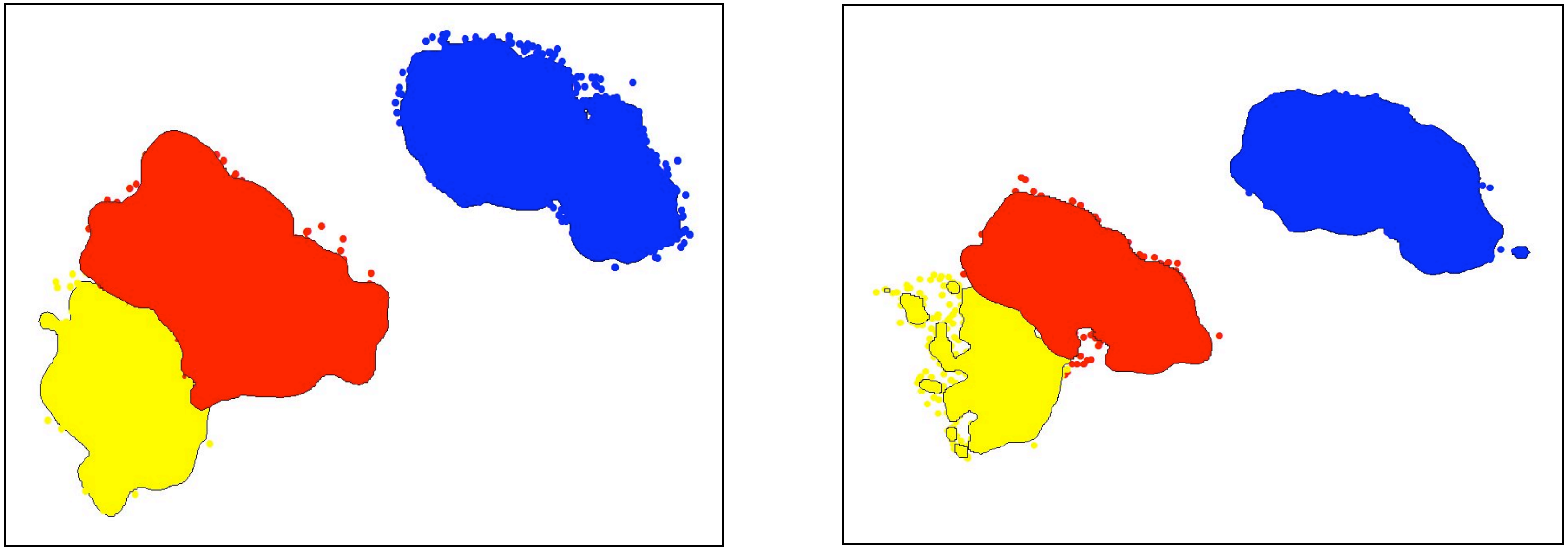


April- August 2004 October 2004- February 2006 April-August 2005



October 2005- February 2006 April- August 2006 October- December 2006

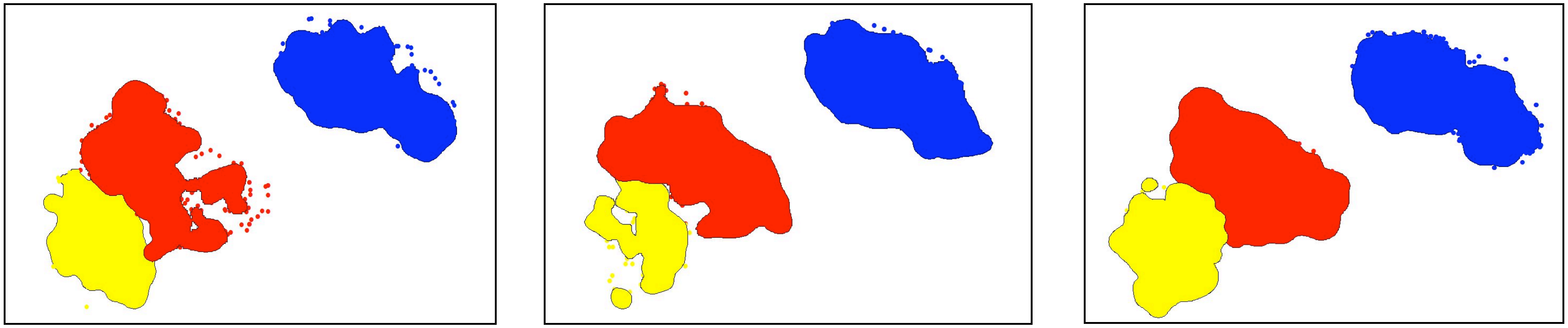
Fig. 1.9



Mating season

Birth season

Fig. 1.10

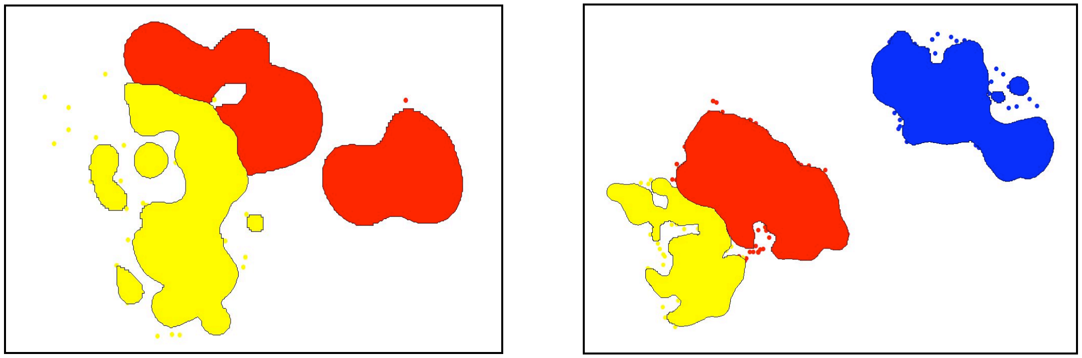


1st Mating season

2nd Mating season

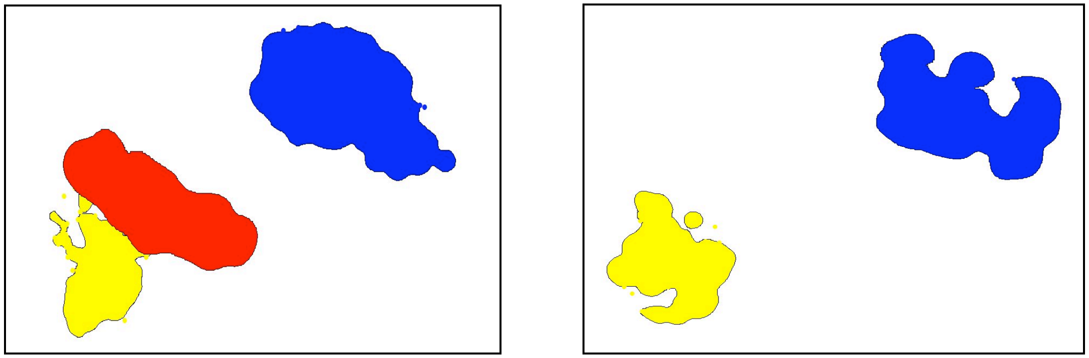
3rd Mating season

Fig. 1.11



1st Birth season

2nd Birth season



3rd Birth season

4th Birth season

Chapter 2: Daily path length and territoriality in Phayre's leaf monkeys

ABSTRACT

There are currently two different methods of calculating defensibility of non-human primate home ranges. This study investigates both methods, and also tests for differences in the defensibility of a home range when seasonal range use is taken into account, versus undifferentiated use of all available data to determine defensibility. Because leaves are not seen as an economically defendable resource, folivorous primates are not usually considered capable of, or motivated to defend home ranges. This examination of defensibility in an Asian colobine, *Trachypithecus phayrei,*, which is known to exhibit territorial behavior, may provide a useful basis for examining home range defensibility in other colobines, particularly in relation to seasonality, and bring up possible reasons for territoriality that are not directly food-related. In addition, there is little scientific consensus about what constitutes territorial behavior and true territoriality in primates. Hence, a detailed literature review and discussion follow about territoriality, specifically the link between diet, territoriality and defensibility in colobines, along with certain suggestions for criteria to determine defensibility in non-human primates.

I obtained different results with each method of calculating defensibility. When I used Mitani and Rodman's (1979) *D* index of defensibility, groups were rarely found to be capable of home range defense, but when I calculated defensibility with Lowen and Dunbar's (1984) *M* index (which takes into account the distance at which conspecifics can be detected), all three groups were able to defend their ranges 100% of the time. Because I obtained such different results with each method, differences in seasonal defensibility were difficult to distinguish. Although two of the three groups had higher *M* indices when seasonal values were calculated, the same did not hold true for the third group. Regardless, calculating seasonal indices of defensibility is a useful basis for further investigation for non-human primate species, in particular to discern reasons why certain species exhibit territoriality and the link between diet and defensibility as well non-food related territoriality and defensibility. This may provide an important basis for further research into defensibility, particularly in other folivorous species.

INTRODUCTION

The term 'territory' may be used to distinguish the area within a home range that is more or less exclusively occupied by an individual or group, and is defended against encroachment by conspecifics through defense, display or advertisement (Noble 1939; Burt 1943; Lincoln et al. 1982). In some non-human primate species with little to no overlap in home range, territories may be deemed to be nearly as large as, or synonymous with home range. Other species, however, have only a small 'core area' of their home range that may be considered a territory, or lack any exclusive territory whatsoever.

Current methods of calculating defensibility in non-human primates are based on how well individuals or groups can cross their home ranges and monitor the boundaries of those ranges to prevent intrusion by conspecifics. Assuming that the home range is roughly circular, if a group's average daily path length (the distance that a group travels within 24 hours, is large enough to cross the diameter of their home range, the home range is defensible (Mitani and Rodman 1979; Lowen and Dunbar 1994).

Typically, folivorous primate groups are considered incapable of maintaining average daily path lengths that allow them to defend their home ranges. Brown (1964) stated that competition for limited resources is the basis for territoriality to evolve and that those limited resources must be spatially distributed so that they are defensible (Brown 1964; Mitani and Rodman 1979). However, due to the supposedly even distribution and widespread availability of leafy plants in most habitats, compared to that of fruits, folivore food supplies were, until recently, considered to be neither extremely limited, nor "economically defendable" (Brown 1964; Mitani and Rodman 1979; Wrangham 1980; Janson and van Schaik 1988). That is to say, the costs of such defending resources within the home range would outweigh any benefits accrued from those resources through the process of defense. However, as there is no benefit to such defense (as is assumed for leaves), than there is no point in engaging in defensive behaviors. Consequently, in densely populated areas, home ranges of conspecific folivore groups may significantly overlap each other and between-group encounters are not expected to be particularly aggressive (Janson and van Schaik 1988).

However, more recent studies indicate that this classification of folivore primates is too simplistic. Some studies have shown that even access to leaves may be contested (Koenig et al. 1998) and folivores may experience between-group contest competition (Koenig 2000). Other studies have indicated or suggested that folivores may even exhibit male resource defense (Fashing 2001b; Harris 2005). Still, all of these populations are rather "non-territorial" with a rather high home range overlap. But previous studies indicate that Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) conform even less to the traditional suggestions on folivores., in that they maintain home ranges with very little overlap and exhibit extremely territorial behavior.

A further obstacle in investigating territoriality and defensibility is that there is little consensus of what actually constitutes territoriality in non-human primates. There is a lack of agreement in the literature on the definition territorial behavior or what criteria need to be fulfilled for a species to be classified as territorial, including how much overlap in group home ranges is acceptable. Therefore, some investigators may classify one species' behavior as territorial, while others would not.

There are currently two different methods of calculating home range defensibility in primates. In 1979, Mitani and Rodman published the first paper that presented a possible means of quantifying whether or not home ranges were defensible, building upon Waser's (1976) "gas models" to assess between-group encounter rates in mangabeys. Waser's (1976) kinetic gas model is based on simple kinetic collision theory which regards the forest (or, in general, the species' habitat) as a two dimensional gas consisting of n primate groups. The collision, or approach, frequency of groups within a certain distance is dependent on both group density (d) and the velocity (v) at which independent groups move. Should groups approach each other less frequently than determined by the mode, mutual avoidance and/or site-attachment is likely present. Likewise, if group encounter rates and approaches are higher than expected, it is likely that groups are actively seeking one another, perhaps for the purpose of territory defense (Waser 1976; Barrett and Lowen 1998).

Following this, Mitani and Rodman (1979) noted that the ability to monitor for, and defend a given area against potential conspecific intruders, is dependant upon the frequency with which an animal or group encounters the perimeters of its range (assuming the range is circular). The frequency of encounters with the boundaries of an area can be expressed as a function of the relationship between day range (or daily path length) and the size of the home range. In other words, it is indicative of the mobility that an animal has within its home range, and how often it can cross between home range boundaries. A small day range relative to home range size implies that an animal is unlikely to come into contact with the perimeters of its home range on a daily basis, and is consequently unable to prevent conspecifics from coming into, and potentially utilizing resources in its home range. Conversely, when daily path length is long relative to home range size, an animal is prone to frequent contact with the borders of its home range, and is able to patrol for, and defend against encroachment by conspecifics (Mitani and Rodman 1979).

Taking into account this ratio of day range length to home range size, Mitani and Rodman quantified defensibility (or 'defendability,' as they prefer to call it) as:

$$D = d/d'$$

where D is the 'index of defendability' (*i.e.* the ability of an animal to monitor the borders of its home range), d is the average day range length, and d' is the diameter of a circle that is equal in area to the observed home range (denoted as A). Thus,

$$d' = (4A/\pi)^{0.5}.$$

An index of defendability that is equal to, or greater than 1.0 signifies that an animal may cross the diameter of its home range one or more times per day, which Mitani and Rodman deemed to be, "somewhat arbitrary…[but] a reasonable lower limit on monitoring in order to maintain exclusive use of a range." (Mitani and Rodman, 1979; p. 243). D- indices of less than 1.0 are therefore taken to distinguish animals or species that cannot maintain exclusive access to a home range by defending it against conspecifics.

Mitani and Rodman (1979) then classified primate species according to defensibility indices of less than, or greater than (or equal to) 1.0, noting also whether species were characterized as territorial or non-territorial. In their original analysis, they found that few non-territorial species exist with defensibility indices equal to, or greater than 1.0, and that no territorial species exist who have defensibility indices that are less than 1.0. Lastly, Mitani and Rodman (1979) noted that, when sorted by group weight and diet, there was no difference in daily path length between territorial and non-territorial species. They took this to indicate that foraging and feeding requirements are the chief determinant of daily path length. Therefore, home range size is the primary limitation on defensibility and primates will only defend a home range if the distribution of food and their foraging regimes allow them to do so (Mitani and Rodman 1979).

Lowen and Dunbar's (1994) critical examination of Mitani and Rodman's index of defensibility noted that D fails to take into account anything other than daily path length and home range diameter, thus assuming that territory defense is solely dependent on how often the animal or group crosses its territory (rather than auditory or visual ways in which groups patrol home range boundaries). Lowen and Dunbar (1994) also found that not all non-territorial species had a D index equal to less than 1.0, but that $D = 0.98$ is a better predictor of whether a species is territorial. Lowen and Dunbar (1994) argued that the length of the range boundary, as well as the animal, or group's, ability to monitor portions of the boundary at a give location, and hence the number of fixed-length boundary sections that must be visited, is also critical to determining defensibility.

Taking this factor into account, Lowen and Dunbar (1994) presented a new defensibility index, M, or the "fractional monitoring rate", which takes into account the portion of home range boundary that the animal or group can monitor at each boundary collision. Hence,

$$M = N(sv/d^2)$$

in which N is the number of independently moving "foraging parties" in the home range (to account for species with a fission-fusion system), s is the detection distance at which the animal or group can perceive conspecific intruders, v is the mean daily path length (*i.e.* velocity in terms of km/day) and d is the diameter of the circle whose area is equal to that of the home range. While a $D \leq 1.0$ (or 0.98) is the critical measure of defensibility set by the Mitani-Rodman index, M must be at least equal to 0.08 for a species to be capable of territory defense.

However, it is important to note that although M takes into account detection distance, it still is not a perfect predictor of whether or not a species is territorial. In a table of species listed in Mitani and Rodman's (1979) paper where the authors originally compared D to ranging, feeding and between-group behavior in 33 primate species, D was inconsistent with whether or not a species is territorial in 14 of 49 cases (29% failure rate), while M failed to predict whether or not a species is territorial in 10 cases (20% failure rate) (Lowen and Dunbar 1994). Furthermore, while both papers make use of ranging data from several different studies of primate species, neither Mitani and Rodman (1979) nor Lowen and Dunbar (1994) specified standards for the length of studies from which they calculated defensibility.

Mitani and Rodman (1994), in particular, addressed the link between diet and defensibility. Phayre's leaf monkeys does not fit Mitani and Rodman's criteria for being able to successfully patrol the perimeters of, and defend their home range. Their home ranges appear to be relatively large (Gibson & Koenig in revision) compared to their daily path length (Chapter 1). This would fit a non-territorial pattern and an expected D smaller than 1 and an expected M smaller than 0.08. However, behavioral data show that Phayre's leaf monkeys maintain separate home ranges with little overlap (Gibson & Koenig in revision). Additionally, between-group encounters are extremely aggressive, and consist of displacements, chasing and even biting or scratching, contradicting the pattern typically seen in primate species wherein territorial behavior and the ability to defend a territory are linked (Koenig- *pers. comm.*,; Brown 1964, 1982; Wrangham 1980). While Waser's model was strictly defined in spatial, rather than behavioral terms, the lack of home range overlap and the behaviors exhibited by *T. phayrei* during agonistic interactions may indicate at least some degree of territoriality (Waser 1976, Barrett and Lowen 1998).

There might be several, not mutually exclusive, potential explanations for the seeming disconnect between behavior and defensibility in *T. phayrei.* First, while the defensibility index D is easily inferred and might indeed indicate non-defensibility, using *M*- indices instead of *D*- indices may yield different results, as *M* takes into account the detection distance of the group at range boundaries. As pointed out by Lowen and Dunbar (1994; see also above), the M index has provided a better match between territoriality and defensibility.

Second, regardless of method, primate group defensibility indices are typically calculated using all available ranging data collected by the researcher (i.e. data used may range from 3 months to 5 years). However, total range for a primate group is unlikely to remain constant throughout the year (and range sizes may expand or contract from year to year). Although for most primates it is fair to assume that home ranges are fairly stable (Mitani and Rodman 1979) an increase in range size or a shift in range over years might indicate larger ranges than actually exist. This would lead to smaller *D* or *M* values than if annual values would have been used.

In addition, during a given year ranges may shrink or contract in response to the availability of such resources as food, temperature and rainfall, group composition, or receptive females (Cheney 1987). Likewise the daily travel distance may vary throughout the year, so that the "true" defensibility might only be indicated by certain periods of the year. For example, Bartlett (2009) showed that the D index varies for white-handed gibbons throughout the year so that male should be able to defend more than one females. But during certain periods of the year home range size and day range are such that a male is capable of defending only one female. Since males may defend resources or females, the main reason for territoriality could be either of these "resources" and an analysis of defensibility should take both into account.

The purpose of this study was to investigate whether *T. phayrei* actually are capable of home range defense, and what resources they may be defending. Hence, here I investigated the relationship between home range, day range and defensibility of a home range as considered by both Mitani and Rodman (*D*) and Lowen and Dunbar (*M*) by including possible differences in the defensibility of a home range when indices are calculated on a seasonal basis. In order to understand the interaction between home range and daily path length in relation to such factors as seasonality, habitat quality and group size, I decided to calculate average daily path lengths and defensibility indices for: 1) Extended periods of time and; 2) Three different types of "seasons" that could lead to significant differences in daily path lengths.

In addition, I investigated the possibility that calculating defensibility on a seasonal basis may show that *T. phayrei* groups may be able to defend their home ranges at certain times of year, depending on the availability of the resource that they are defending. I used my results to judge whether one method of calculating territoriality is better than the other. I also discussed the relationship between territoriality and defensibility, reviewed the literature on territoriality, and presented possible criteria to determine territoriality in non-human primates, particularly in colobines. These findings may provide an important basis for further investigations into the defensibility, territoriality, seasonality and the relationship between the three in non-human primates, particularly in colobines.

METHODS

Field site and study species:

Data for this study were collected at the Phu Khieo Wildlife Sanctuary (hereafter abbreviated as PKWS), located in the Chaiyaphum province of Northeastern Thailand. The sanctuary covers an area of 1,573km^2 and is located at 16°05- 35'N latitude, and 101°20-55'E longitude, with elevations above sea level ranging from 300- 1,300m (Khon Kaen University and Phu Khieo Wildlife Sanctuary 1995; Koenig et al. 2004). PKWS is primarily composed of hill and dry evergreen forest, with patches of dry dipterocarp forest (Borries et al. 2002). A single paved road passes through the sanctuary, demarcating the southern edge of the study site (Gibson and Koenig in revision). Average temperatures at PKWS range from 17-25°C, and monthly rainfall ranges from 0-275 mm. PKWS contains a high diversity of fauna, including several primate species.

Trachypithecus phayrei (common name, Phayre's leaf monkey or Phayre's langur) is a highly folivorous colobine species, ranging throughout Bangladesh, Burma, India, Thailand and Vietnam (Groves 2001). Phayre's leaf monkeys are found in both uni-male and multi-male groups, and are sexually dimorphic, with females weighing about 6.3 kg and males about 7.9 kg (Gupta and Kumar 1994; Fleagle 1999). Group sizes range from 3-30 individuals, and home ranges have been suggested to be relatively small (Gupta 2002). Although female *T. phayrei* exhibit linear dominance hierarchies (and possibly an age-inversed hierarchy), they are not philopatric and often disperse to other groups during between group encounters (Borries et al. 2004; Koenig et al. 2004a). Males exhibit affiliative behavior quite frequently associating with each other and occasionally caring for infants (Koenig et al. 2004b).

Habituation at PKWS started in October 2000. Each group took approximately one year to habituate, and although the data included in this study are taken from three focal groups (PA, PB and PS), there are currently four habituated *T. phayrei* groups within the sanctuary. Groups (see Chapter 1, Table 1.1) consisted of one or more adult males and circa seven females, along with immature members (average 16.3 individuals) (Koenig et al. 2004). PA was a multi-male group, and consisted of 16-22 members during the period of study. PB and PS were single-male groups. PB was by far the largest group (24-31 members from March 2004 to December 2006), while PS contained the fewest number of members (ranging from 9-16 individuals).

Although inter-group encounters are rare in the study population, *T. phayrei* show little overlap in home ranges between groups and exhibit a wide range of territorial behaviors when inter-groups encounters occur, including vocalizations, displays, chases, and even aggressive physical contact (Gibson and Koenig in revision). While males are typically the chief participants in these behaviors, female dispersal takes place during inter-group encounters as well; the observed lack of aggressive female participation in territorial behaviors may also be due to the fact that females take longer to habituate than males, and may be more reluctant to descend to the ground in the presence of researchers. Males also emit a 'whoop' long call that may function both within and between groups to regulate spacing (Koenig and Borries, *pers. comm.*).

Data collection:

Ranging data for this study were collected from continuous all-day follows, where GPS data points were taken at first contact with the group, and subsequent data points were taken every thirty minutes, on the hour and the half-hour. GPS points were taken at the approximate center of a group. Home ranges for each group were calculated from all available, sufficiently accurate data (GPS error below 10 m) for the study period of March 2004- December 2006. Day ranges were taken only from "full days", in which no more than three data points were missing per day (Tables 1.2-1.4 show the number of full days in each season). Due to changes in day length, the definition of "full day" varied throughout the year. From March to September of each year, the first data point in a full day could be taken no later than 6:30 and the last point no earlier than 18:00. During October to February, the first point must have been taken no later than 7:00 and the last point no earlier than 17:00. On average, each group was followed for ca. 5 days per month. However, due to a separate research project, group PB was followed more extensively throughout late 2005 and the majority of 2006, hence more data were available for PB than for PA or PS.

Data analysis:

Typically, researchers include all available ranging data when calculating home range size, daily path length and defensibility without accounting for any type of seasonality. Published studies that include defensibility indices for primate populations use ranging data that spans anywhere from six months to several years. While calculating *D*-indices and *M*- indices for all available data and for individual years, I also included seasonal subdivisions.

Season 1:

The climate at PKWS varies throughout the year, but may be divided into two general seasons: 1) hot and humid, with substantial rainfall, or 2) cold and dry, with little rainfall (Table 1.5). *T. phayrei* group home ranges may contract in response to colder temperatures, due to the shorter length of days that generally occur at the same time as such temperatures and the increased loss of energy associated with extensive travel. Hence, larger average daily path lengths and/or smaller ranges may lead to varying defensibility throughout the year.

Mean temperature from January 2004 - December 2006 was 21.41°C (95% CI= 20.86-21.96 °C). Average rainfall for PKWS was 86.75 mm per month (95% CI= 59.86-113.65 mm; see Chapter 1, Table 1.5). To differentiate between the hot, humid and cold, dry seasons, I placed all months with rainfall measuring less than 59.86 mm into the cold and dry category. Although temperatures did vary with the seasons, the range of variability was smaller and did not always coincide with rainfall changes, making divisions somewhat less clear. Hence, temperature was not used as the main criterion for differentiating between seasons. Thus, hot and humid seasons had a temperature range of 19.75-24.06°C, with a mean of 22.38°C, and rainfall ranging from 65.78- 241.12 mm with a mean of 134.38 mm. Cold and dry seasons had a temperature range of 16.56-23.32°C, with an average temperature of 19.58°C, and rainfall ranging from 0.00- 42.02 mm per month, with a mean of 10.73mm.

Season 2:

Because *T. phayrei* is a colobine species (more than 40% of its food intake is made up of leaves), and leafy plants are liberally distributed throughout PKWS, food defense initially seems energetically wasteful and ultimately futile (Brown 1964; Wrangham 1980). However, there is the possibility that males defend home ranges (and areas of intensive feeding in particular) in order to attract and keep adult females in the group (Emlen and Oring 1977; Wrangham 1980; Borgerhoff Mulder 1987a,b, in Harris 2005; Fashing 2001 a,b; Harris 2005). Furthermore, because *T. phayrei* females disperse from the group, male defense of the home range in order to increase female reproductive success may prove to be a successful mating tactic.

Phenology data (Koenig and Borries, unpublished data) for flowering, fruiting and leafy plants show that the months of April through August can be characterized as "lush" for all three years in this study, in which the percentage of trees bearing young and mature leaves and fruits peaks and food availability is high, while October through February are months of low food availability, i.e., lean season. March and September were not included in either season, because they did not clearly fit into either the lean or the lush categories.

Season 3:

While calculating *D*-indices and *M*- indices for Season 2 may indicate indirect male mate defense of females, variability of defensibility in Season 3 may point to direct male mate defense (Trivers 1972; Wrangham 1980; Harris 2005). During a mating season all members in a group, and male individuals in particular, may expand their daily path lengths and patrol the boundaries of their home range more vigilantly, either to keep out conspecific intruders or looking to mate with females within the group, or in order to pursue females in order to copulate with them themselves. Conversely, newborn and extremely young infants may restrict ranging of their mothers in particular and the group in general. However, a further possibility associated with infant births is that the daily path length actually *increases*, as females range further to satisfy the increased nutritional needs associated with lactation. The birth season was extrapolated here from the known distribution of births in a given group and year. In contrast, the mating could only be inferred by subtracting the approximate gestation length (in *T. phayrei* 200 to 210 days; Koenig & Borries *pers. comm.*) from birth dates, therefore estimated mating periods used in this study may be overly conservative.

I then calculated both *D*- and *M*-indices for all overall, yearly and seasonal home ranges. As previously mentioned, the formula d'/d is used to obtain Mitani and Rodman's defensibility index (*D)* (Mitani and Rodman 1979). For Lowen and Dunbar's defensibility index (*M*), the formula used ($M = N(sv/d^2)$) takes into account detection distance of a group (s) at the home range boundary, not simply the frequency with which the group crosses the home range. For *T. phayrei* at PKWS, I set s equal to 150 meters, a fairly conservative approximation, as *T. phayrei* appear to be able to hear and detect conspecifics from as far away as 200-300m (Koenig and Borries *pers. comm.*).

RESULTS

Tables 2.1 through 2.8 show home range size, daily path lengths, as well as *D*- and M- indices for overall, yearly and seasonal ranges. For each season, I calculated both types of defensibility index for 1) the 95% Kernels of the complete home range area of each group (PA = 1.071 km^2, PB = 0,950, PS = 0.580); and 2) 95% Kernels of each groups' range on a seasonal basis.

Complete and yearly home ranges:

Tables 2.1 and 2.2 show *D*- and *M*-indices for PA, PB and PS for complete home ranges and average DPLs from 2004-2006, as well as ranges and average DPLs calculated on a yearly basis. A *D*-index of greater than or equal to 0.98 was taken to indicate the ability to defend a home range, while the same was considered true for the an *M*-index of 0.08 (Mitani and Rodman 1979; Lowen and Dunbar 1994). Neither the PA nor the PB group was capable of home range defense based on *D*-indices calculated using all available data. When *D*-indices were taken from average yearly DPLs, PA was shown to be capable of home range defense in 2004, and also had a *D*-index of 0.98 in 2006 when the *D*-index was calculated using overall home range, but not the increased home range area used by the group in 2006 alone. PB had only one *D*-index greater than 0.98, occurring in 2004 when *D*-index was obtained based on yearly range in 2004 (less than overall home range from 2004-2006). Lastly, PS was capable of home range defense at all times using Mitani and Rodman's *D*-index.

Conversely, *M*-indices calculated for all three groups based on both complete and yearly bases, using an *s* (conspecific detection distance) of 150 meters, indicated that all groups were fully capable of home range defense.

Season 1:

When *D*-indices were calculated for all three groups using both the complete home range and seasonal ranges based on temperature and rainfall, PA was capable of home range defense less than half the time, PB had *D*-indices greater than 0.98 only during the hot and humid season of April- September 2004, and PS was capable of home range defense for the majority of the seasons (Tables 2.3 and 2.4).

Although PA and PS showed slightly larger *D*-indexes (and both larger average DPLs and larger seasonal ranges) for the hot and humid seasons than for cold and dry seasons, these differences did not alter PA's capacity for home range defense. The three cases in which PS was unable to defend its home range, however, are limited to *D*-indices calculated for cold and dry seasons, using the complete home range for 2004-2006. PB showed no consistent pattern in seasonal range or seasonal average daily path length. While *D*-indices from PS and DPLs and range size from PA indicate a contraction of range size and daily path length during seasons of colder temperatures and decreased rainfall, these results are insufficient to show a link between defensibility and Season 1 based on Mitani and Rodman's *D*-index.

However, *M*-indices showed that all three groups were capable of home range defense regardless of differences in temperature or rainfall. Furthermore, there was no consistent direction showing that *M*-indices were greater during hot and humid periods versus cold, dry seasons.

Season 2:

D-indices calculated for PA using the complete home range showed capability for home range defense in only one instance: for the lush period of April- August 2004 (Table 2.5). However, when *D*-indices were calculated from seasonal home ranges, PA appeared to be capable of defending its range during all lean seasons, but only during one lush season (again in April- August 2004; Table 2.6). Although PB was incapable of home range defense at any period when lean and lush seasons was used as the basis for calculating *D*-indices and there was no consistent direction in *D*-indices calculated using complete home range size, *D*-indices (though still not equal to or above 0.98) were greater during lush seasons than lean seasons. Finally, PS had *D*-indices of 0.98 or greater for nearly all lush and lean seasonal divisions, with the exception of April-August 2005, when the *D*-index was calculated from complete home range area. There also appeared to be no consistent direction of decrease or increase in *D* based on food availability.

Once again, *M*-indices for all three groups were above 0.08 at all periods during Season 2. Hence, there appeared to be no correlation between defensibility and food availability throughout the year.

Season 3:

D-indices calculated for PA showed that PA was capable of home range defense far less than half of the time when *D* was calculated on the basis of mating and birth seasons (Table 2.7 and 2.8). Furthermore, there was no consistent distinction between defensibility in either mating or birth seasons. As in other seasons, *D*-indices calculated for PB only showed capacity for home range defense during one period (March 2004, when *D* was calculated using seasonal home range). PS, consistent with Seasons 1 and 2, had *D*-indices that were at or above 0.98 for the majority of the time, and was only incapable of territory defense during the mating period of October 2004 through May 2005. Consistent with previous seasons, *M*- indices never fell below the threshold of defensibility, and there was no apparent directionality of increased or reduced defensibility on a seasonal basis. This discrepancy between results from D- and M-indices was, in fact, present for all calculated defensibility indices.

DISCUSSION

Having obtained *D* and *M* indices for *T. phayrei* at PKWS, the purpose of the following discussion is four-fold: 1) based on the above findings, to determine if either method of calculating defensibility is more valid, 2) to discuss various problems regarding territoriality and its varying definitions within the scientific literature; 3) to address the relationship between territoriality and defensibility of a territory, and; 4) to discuss, in a general sense, the relationship between territoriality and defensibility in other colobine species.

The extremely different results obtained by each method of calculating defensibility makes comparison difficult. Based on *D* and *M* indices for all three groups, there appears to be little correlation between seasonality and defensibility. When defensibility was calculated using *M* indices, all three groups were categorized of being capable of home range defense regardless of temperature, rainfall, food availability or mating and infant birth patterns. Additionally, the fact that all *M* indices were above 0.08 made it difficult to distinguish whether *M* indices calculated from seasonal home range use are consistently higher than those calculated using the complete set of home range data spanning from 2004-2006 (Table 2.9). For the most part (PA and PS) *M* indices were indeed larger using seasonal home ranges, but that was not true for the third group PB.

In contrast, the results obtained by using Mitani and Rodman's formula for *D* indices were chiefly dependent on the group that was being examined (Table 2.14), in which PS members were consistently able to defend their range, PA members were able to defend their home range between 30-40% of the time, and PB was rarely capable of home range defense. However, all three groups showed higher rates of viable home range defensibility when *D*-indices were calculated using 95% Kernel areas of seasonal range use rather than complete home range (Table 2.14), and it appears that there may be some correlation with lush seasons and higher defensibility, that is to say that DPLs increase relative to home range in periods when food (or preferred, patchily distributed foods) are more abundant. This may further indicate that *T. phayrei*, like certain other primate species, copes with relatively low food availability (or quality) by reducing foraging efforts and conserving energy with smaller DPLs (Di Fiore 2003a).

Hence, my prediction that defensibility indices would be positively correlated with group size was not supported by the data. To the contrary, PS was most consistently capable of home range defense when *D*-indices were used to judge defensibility. While defensibility may be correlated with seasons of lush food availability, the calculation of *D*- indices does not indicate that *T. phayrei* groups were more capable of defending their home ranges during seasonal periods that were based on either temperature or mating and birth patterns.

Lowen and Dunbar's (1994) *M*-index has a clear advantage over Mitani and Rodman's (1979) *D* in that it takes detection distance into account. The results shown here are also consistent with the behavior of Phayre's leaf monkeys and it was consistent over all periods. However, the results shown here do not determine clearly whether it is a better and more accurate measure of defensibility than that conceived by Mitani and Rodman. *T. phayrei* at PKWS clearly exhibit agonistic behavior toward conspecifics, yet the economic defensibility of their diet remains suspect. Hence, it is impossible to say whether either method is conclusive until more comparative studies of this nature have been carried out while taking territorial behavior into account.

One possible step toward resolving issues of defensibility in *T. phayrei* would be to measure habitat quality at the core of each group's home range, relative to habitat quality at the boundaries of the range. Should the quantity and/or quality of food at the core be greater than that at the boundaries, home range defense is likely advantageous (Brown 1964, 1982). Another method of discerning the motivation for territoriality might be to examine frequency rates and aggression of inter-group encounters relative to seasonality (i.e. are encounters and the aggression seen driven by the presence of receptive females, or by food availability?) (Harris 2007). Yet another possibility is that small uni-male groups, such as PS, operate differently than larger and multi-male groups, in order to defend females by maintaining a home range size that is far smaller and hence boundaries that are easier to monitor for and defend against conspecific intruders (Gibson and Koenig in revision).

A more fundamental question, however, is how to scientifically define territorial behavior. Although both *D* and *M* defensibility indices differentiate fairly well between species classified as exhibiting 'territorial' or 'non-territorial' behavior (but see Yeager & Kool 2000; van Schaik etal. 1992), the problem remains that there is no standard definition for either 'territory,' or a set of criteria that defines 'territoriality.' Although Mitani and Rodman (1979) briefly noted the lack of a fixed definition of 'territoriality,' for their analyses, they "accepted the judgment of the investigator" (p. 243), when classifying species' behavior. While Lowen and Dunbar (1994) reiterated the importance of including territorial behavior as a factor in a species' ability to defend its territory, they also neglected to address the lack of consensus on what constitutes such behavior. Hence, a comprehensive literature review of territory and territoriality follows, as well as a set of possible criteria for defining territoriality.

The term 'territory' may be used to distinguish the area within a home range that is more or less exclusively occupied by an individual or group, and is defended against encroachment by conspecifics through defense, display or advertisement (Noble 1939; Burt 1943; Lincoln et al. 1982). In some primate species with little to no overlap in home range, territories may be deemed to be nearly as large as, or synonymous with home range. Other species, however, have only a small 'core area' of their home range that may be considered a territory, or lack any exclusive territory whatsoever.

When one investigates the idea of territory, whether in primates or other animals, a central concern is how an animal, or group of animals, maintains exclusive access to an area and prevents intrusion by conspecifics. Although the concept of 'territorial behavior,' or 'territoriality' may seem to be a simple one at first glance, it is anything but. In a review of the various definitions of territorial behavior Maher and Lott (1995) found forty-eight different conceptualizations of territoriality, with the widest range of definitions found in mammalian studies. Although the two most commonly used definitions of territoriality was the maintenance of a 'defended area' or 'site-specific dominance', consensus on an explicit definition was rare ('defended area,' the most popular definition was used in only 50% of papers).

Along with a lack of consensus on a scientific definition, different researchers often used a varying number of criteria to confirm territoriality, depending on the taxonomic order of animal studied and the data that are available. In one sense, the degree of flexibility in the definition of territoriality is advantageous, as it allows for broad comparisons among species and the inclusion of more subtle forms of territory defense (e.g. scent-marking). However, lack of a clear definition also makes it difficult to determine if behaviors other than true territoriality and conspecific aggression are actually at work, such as mutual avoidance (Maher and Lott 1995).

The earliest definitions of territoriality, as conceived within socioecological and sociobiological constructs, originate from avian studies. While certain researchers defined territoriality by exhibited behaviors related to the defense of an area with the purpose of excluding other individuals, other definitions took a strict, outcome-based approach, in which exclusive use of an area was necessary, regardless of the behaviors and interactions leading to such exclusivity (Noble 1939; Pitelka 1959; Maher and Lott 1995). While the second conceptualization is useful in that it presents a very clear idea of what constitutes territorial behavior, and links such behavior to a definitive outcome, it potentially excludes behaviors that ultimately result in the maintenance of an exclusive area through more subtle means. Furthermore, the question remains of what, precisely constitutes ‘exclusive use’? Should there be absolutely 0% overlap of conspecific groups, or should a threshold percentage of 10-25% overlap be accepted?

At the opposing end of the spectrum that encompasses definitions of territoriality lies the concept of territorial behavior as ‘respect for the ownership’ of an area by a conspecific group (Kummer 1995). This characterization of territorial behavior is not based upon active defense of a territory, but instead upon mutual avoidance by conspecific groups of each other’s home ranges or core areas. Although this particular definition certainly takes into account the finer and less obvious points of how animals may maintain exclusive access to a particular area within an environment, it is difficult to generate criteria for this behavior that distinguish it from avoidance behaviors that may arise for alternative reasons.

Many definitions of territoriality exist that lie between these two extremes. They range from describing territorial behavior as denoted by direct forms of intergroup interaction, involving agonistic or aggressive behavior between conspecifics at the boundaries of a territory (such as physical violence, display, chases and vocalizations), to indirect forms of communication regarding ownership of an area (*e.g.*, long calls or scent marking), that may regulate the spacing of conspecific individuals or groups, to the decidedly general, ‘behavior related to the defense of a territory’ (Maher and Lott 1995; Lincoln et al. 1982). One should note that these definitions do not inextricably link territorial behavior to the unequivocal defense or monopolization of an area.

A further problem with establishing territoriality is the number of necessary criteria to be satisfied. For example, the sole criterion may be the existence of an area of exclusive use, as in Pitelka (1959), or there may be multiple (usually no more than three) criteria, as in Wittenberger (1981, in Maher and Lott 1995), where: “some or all activity was restricted to a defended area, one’s presence was somehow advertised in that area, and the animal maintained essentially exclusive possession of all parts of an area.”

Finally, Brown (1964) states that the evolution of territorial behavior in a species is depended on competition for limited resources in an area, and ultimately relies on whether those scanty resources are ‘economically defensible’. That is to say, the benefits gained from successful defense of those resources must outweigh the energetic costs of defensive behaviors. Taking this and the above literature into account, I suggest that the following circumstances must be met to characterize primate species' behavior as "territorial."

1) Conspecific group home ranges show little to no overlap (i.e. less than 20%)
2) Between group encounters should occur at home range boundaries
3) When between-group encounters occur, individuals in each group exhibit *high* degrees of agonistic behaviors such as:
    a. Loud, repeated vocalizations
    b. Chasing, lunging, jumping and displacements
    c. Physically violent behavior such as biting, scratching or jumping on conspecifics
4) A limiting and 'economically defensible' resource (or at least a possible limiting resource) must exist, whether consistently or seasonally

As stated above, additional evidence for successful territory defense may be found by comparing food quality at the core of the group's home range versus the borders. If qualitative and or quantitative differences are found, a strong case may be made for economic defensibility of a territory (Brown 1964; Fashing 2001 a,b; Harris 2005). Moreover, it is undeniable that further problems remain surrounding investigations into territoriality. For example, even the definition of aggressive, between-group encounters are unclear and show marked variation between studies (Cheney 1987; Harris 2007; Wich & Sterck 2007; Wilson 2007).

Drawing upon the point that foraging regimes are the primary determinant of daily path length, it is useful to look at defensibility indices for one radiation of primates in which all species adopt an almost uniformly folivorous diet: the colobines. Colobines are predominantly group-living species found throughout Asia and in some areas of Africa. They are estimated to have diverged from their sister taxon, the cercopithecines, about 13 million years ago (Newton and Dunbar 1994; Disotell and Stewart *as cited in* Fleagle 1999).

As shown in Table 2.11, when colobines are grouped according to indices of defensibility and characterized as territorial or non-territorial (according to the investigator), the relationship between territoriality and defensibility to some degree as that found by Mitani and Rodman (Mitani and Rodman 1979). There are, however, several species that exhibit territorial behavior while having *D*-indices of less than 0.98, and/or *M*-indices of less than 0.08 (*M*-indices are calculated using a conservative detection distance of 50 meters as used by Lowen and Dunbar (1994)). In this comparison and contrasting Lowen and Dunbar (1994) the match between defensibity and territoriality is even worse for the *M* index. While in six cases the *D* index did not match, it was 8 for the *M* index. Additionally, evidence for territory defense, through male food defense has previously been found in *Colobus guereza* (Fashing 2001 a,b; Harris 2005). Such data indicate that further investigation of seasonal range defensibility, particularly in colobines may provide new evidence into the relationship between diet, male mating tactics and defensibility, as well as resolving apparent discrepancies between agonistic behavior toward conspecifics and low defensibility indices. Such studies may also provide useful comparisons of the relative merits of *D* versus *M* indices, in particular by providing the true detection distance for each study site. Buzzard (2007) finds *M* indices to be a better method of classification, due to the inclusion of detection distances, but the results of *M*-indices in this study only state that *T. phayrei* home ranges are defensible, without giving an indication of the limiting resource leading to territorial behavior.

Another factor impacting studies of territoriality and defensibility is the length and intensity of studies included. As seen in Chapter 1, ca. 12 months of data collection were necessary to obtain the majority of the home range size of *T. phayrei* groups at PKWS was determined, and range use is highly mutable over various seasons (and even years). Hence, length of study seems to have a high impact on the calculation of defensibility indices and assessments of the correlation between territorial behavior and the ability to defend a home range. Greater selectivity in terms of study length will hopefully lead to more accurate information on defensibility in colobine species in particular, and all primate species in general.

Table 2.1. Home range size, day range length, and defensibility indices on a yearly basis, calculated using overall home range areas for each group.

Group	Year	Home range area [km^2]	Day range length [km]	D	M
PA	All	1.071	1.107	0.948*	0.122
PA	2004	1.071	1.172	1.004	0.129
PA	2005	1.071	1.024	0.876*	0.113
PA	2006	1.071	1.143	0.979	0.126
PB	All	0.942	1.006	0.919*	0.126
PB	2004	0.942	1.025	0.936*	0.128
PB	2005	0.942	1.003	0.916*	0.125
PB	2006	0.942	1.002	0.915*	0.125
PS	All	0.580	0.940	1.094	0.191
PS	2004	0.580	0.969	1.127	0.197
PS	2005	0.580	0.887	1.032	0.180
PS	2006	0.580	0.953	1.109	0.194

*Range is not defensible ($D < 0.98$ or $M < 0.08$)

Table 2.2. Home range size, day range length, and defensibility indices on a yearly basis, calculated using yearly range areas for each group.

Group	Year	Seasonal range area [km^2]	Day range length [km]	D	M
PA	All	1.071	1.107	0.948*	0.122
PA	2004	0.945	1.172	0.948	0.146
PA	2005	1.001	1.024	1.069*	0.120
PA	2006	1.145	1.143	0.907*	0.118
PB	All	0.942	1.006	0.919*	0.126
PB	2004	0.858	1.025	0.936*	0.141
PB	2005	0.986	1.003	0.916*	0.120
PB	2006	0.985	1.002	0.915*	0.120
PS	All	0.580	0.940	1.118	0.191
PS	2004	0.866	0.969	1.238	0.194
PS	2005	0.716	0.887	1.053	0.259
PS	2006	0.904	0.953	1.118	0.175

*Range is not defensible ($D < 0.98$ or $M < 0.08$)

Table 2.3. Season 1 defensibility indices, calculated using overall home range areas for each group.

Group	Year(s)	Month(s)	Home range area [km^2]	Day range length [km]	D	M
PA	All hot and humid seasons	All hot and humid	1.071	1.145	0.980	0.126
PA	All cold and dry seasons	All cold and dry	1.071	1.030	0.882*	0.113
PA	2004	March	1.071	0.728	0.624*	0.080
PA	2004	Apr-Sept	1.071	1.225	1.049	0.135
PA	2004- 2005	Oct-Mar	1.071	1.026	0.878*	0.113
PA	2005	Apr-Nov	1.071	1.034	0.886*	0.114
PA	2005- 2006	Dec-Feb	1.071	1.068	0.914*	0.117
PA	2006	Mar-Oct	1.071	1.178	1.009	0.130
PA	2006	Nov- Dec	1.071	1.033	0.885*	0.114
PB	All hot and humid seasons	All hot and humid	0.942	1.023	0.934*	0.128
PB	All cold and dry seasons	All cold and dry	0.942	0.966	0.882*	0.121
PB	2004	March	0.942	0.833	0.761*	0.104
PB	2004	Apr-Sept	0.942	1.084	0.990	0.136
PB	2004- 2005	Oct-Mar	0.942	0.968	0.884*	0.121
PB	2005	Apr-Nov	0.942	1.027	0.938*	0.129
PB	2005- 2006	Dec-Feb	0.942	1.003	0.916*	0.125
PB	2006	Mar-Oct	0.942	1.006	0.919*	0.126
PB	2006	Nov- Dec	0.942	0.860	0.786*	0.108
PS	All hot and humid seasons	All hot and humid	0.580	1.008	1.174	0.205
PS	All cold and dry seasons	All cold and dry	0.580	0.855	0.996	0.174
PS	2004	March	0.580	0.963	1.121	0.196
PS	2004	Apr-Sept	0.580	0.999	1.162	0.203
PS	2004- 2005	Oct-Mar	0.580	0.836	0.973*	0.170
PS	2005	Apr-Nov	0.580	0.993	1.156	0.202
PS	2005- 2006	Dec-Feb	0.580	0.835	0.972*	0.170
PS	2006	Mar-Oct	0.580	1.043	1.213	0.212
PS	2006	Nov- Dec	0.580	0.833	0.970*	0.170

*Range is not defensible ($D < 0.98$ or $M < 0.08$)

Table 2.4. Season 1 defensibility indices, calculated using seasonal range areas for each group.

Group	Year(s)	Month(s)	Seasonal range area [km^2]	Day range length [km]	D	M
PA	All hot and humid seasons	All hot and humid	1.083	1.145	0.975*	0.124
PA	All cold and dry seasons	All cold and dry	0.964	1.030	0.930*	0.126
PA	2004	March	0.467	0.728	0.944*	0.184
PA	2004	Apr-Sept	0.742	1.225	1.260	0.194
PA	2004- 2005	Oct-Mar	0.701	1.026	1.086	0.172
PA	2005	Apr-Nov	1.075	1.034	0.884*	0.113
PA	2005- 2006	Dec-Feb	0.664	1.0680	1.161	0.190
PA	2006	Mar-Oct	1.143	1.178	0.976	0.121
PA	2006	Nov- Dec	0.981	1.033	0.925*	0.124
PB	All hot and humid seasons	All hot and humid	1.038	1.023	0.889*	0.116
PB	All cold and dry seasons	All cold and dry	0.954	0.966	0.877*	0.120
PB	2004	March	1.915	0.833	0.533*	0.512
PB	2004	Apr-Sept	0.950	1.084	0.986	0.134
PB	2004- 2005	Oct-Mar	0.845	0.968	0.934*	0.135
PB	2005	Apr-Nov	1.067	1.027	0.881*	0.113
PB	2005- 2006	Dec-Feb	1.111	1.003	0.844*	0.106
PB	2006	Mar-Oct	0.943	1.006	0.918*	0.126
PB	2006	Nov- Dec	0.895	0.860	0.806*	0.113
PS	All hot and humid seasons	All hot and humid	0.630	1.008	1.126	0.188
PS	All cold and dry seasons	All cold and dry	0.519	0.855	1.053	0.194
PS	2004	March	0.357	0.963	1.428	0.317
PS	2004	Apr-Sept	0.572	0.999	1.171	0.206
PS	2004- 2005	Oct-Mar	0.488	0.836	1.061	0.202
PS	2005	Apr-Nov	0.487	0.993	1.261	0.240
PS	2005- 2006	Dec-Feb	0.331	0.835	1.285	0.297
PS	2006	Mar-Oct	0.662	1.043	1.136	0.186
PS	2006	Nov- Dec	0.398	0.834	1.169	0.246

*Range is not defensible ($D < 0.98$ or $M < .08$)

Table 2.5. Season 2 defensibility indices, calculated using overall home range areas for each group.

Group	**Year(s)**	**Months**	**Home range area [km^2]**	**Day range length [km]**	**D**	**M**
PA	All lush	All lush	1.071	1.101	0.943*	0.121
PA	All lean	All lean	1.071	1.082	0.926*	0.119
PA	2004	Apr- Aug	1.071	1.184	1.014	0.130
PA	2004-2005	Oct-Feb	1.071	1.040	0.891*	0.114
PA	2005	Apr- Aug	1.071	0.989	0.847*	0.109
PA	2005-2006	Oct-Feb	1.071	1.094	0.936*	0.120
PA	2006	Apr- Aug	1.071	1.127	0.965*	0.124
PA	2006	Oct-Dec	1.071	1.122	0.960*	0.123
PB	All lush	All lush	0.942	1.019	0.930*	0.127
PB	All lean	All lean	0.942	0.987	0.901*	0.123
PB	2004	Apr- Aug	0.942	1.050	0.959*	0.131
PB	2004-2005	Oct-Feb	0.942	0.940	0.859*	0.118
PB	2005	Apr- Aug	0.942	0.997	0.910*	0.125
PB	2005-2006	Oct-Feb	0.942	1.028	0.939*	0.129
PB	2006	Apr- Aug	0.942	1.016	0.928*	0.127
PB	2006	Oct-Dec	0.942	0.963	0.879*	0.120
PS	All lush	All lush	0.580	0.992	1.155	0.202
PS	All lean	All lean	0.580	0.876	1.020	0.178
PS	2004	Apr- Aug	0.580	1.022	1.190	0.208
PS	2004-2005	Oct-Feb	0.580	0.866	1.008	0.176
PS	2005	Apr- Aug	0.580	0.837	0.974*	0.170
PS	2005-2006	Oct-Feb	0.580	0.917	1.067	0.186
PS	2006	Apr- Aug	0.580	1.081	1.258	0.220
PS	2006	Oct-Dec	0.580	0.843	0.981	0.202

*Range is not defensible ($D < 0.98$ or $M < .08$)

Table 2.6. Season 2 defensibility indices, calculated using seasonal range areas for each group.

Group	**Year(s)**	**Months**	**Seasonal range area [km^2]**	**Day range length [km]**	**D**	**M**
PA	All lush	All lush	1.063	1.101	0.947*	0.122
PA	All lean	All lean	1.117	1.086	0.907*	0.114
PA	2004	Apr- Aug	0.759	1.184	1.204\	0.184
PA	2004-2005	Oct-Feb	0.821	1.040	1.017	0.149
PA	2005	Apr- Aug	1.022	0.989	0.867*	0.114
PA	2005-2006	Oct-Feb	0.942	1.094	0.998	0.137
PA	2006	Apr- Aug	1.072	1.127	0.964*	0.124
PA	2006	Oct-Dec	0.981	1.122	1.004	0.135
PB	All lush	All lush	0.977	1.019	0.913*	0.123
PB	All lean	All lean	1.113	0.987	0.829*	0.104
PB	2004	Apr- Aug	0.964	1.050	0.948*	0.128
PB	2004-2005	Oct-Feb	0.922	0.940	0.868*	0.120
PB	2005	Apr- Aug	0.965	0.997	0.899*	0.122
PB	2005-2006	Oct-Feb	1.135	1.028	0.855*	0.107
PB	2006	Apr- Aug	1.003	1.016	0.899*	0.119
PB	2006	Oct-Dec	1.083	0.963	0.820*	0.104
PS	All lush	All lush	0.657	0.992	1.085	0.178
PS	All lean	All lean	0.624	0.876	0.983	0.165
PS	2004	Apr- Aug	0.561	1.022	1.210	0.215
PS	2004-2005	Oct-Feb	0.550	0.866	1.035	0.186
PS	2005	Apr- Aug	0.576	0.837	0.978	0.171
PS	2005-2006	Oct-Feb	0.413	0.917	1.264	0.261
PS	2006	Apr- Aug	0.641	1.081	1.196	0.199
PS	2006	Oct-Dec	0.529	0.843	1.027	0.188

*Range is not defensible ($D < 0.98$ or $M < .08$)

Table 2.7. Season 3 defensibility indices, calculated using overall home range areas for each group. B = birth season, M = mating season.

Group	Year(s)	Month(s)	Home range area [km^2]	Day range length [km]	D	M
PA	All mating seasons	All mating	1.071	1.152	0.987	0.127
PA	All birth seasons	All births	1.071	1.011	0.866*	0.111
PA	2004	March (B1)	1.071	0.728	0.623*	0.080
PA	2004	Apr-Dec (M1)	1.071	1.183	1.013	0.130
PA	2005	Jan-Aug (B2)	1.071	1.004	0.860*	0.110
PA	2005-2006	Sept-Feb (M2)	1.071	1.116	0.955*	0.123
PA	2006	March (B3)	1.071	1.203	1.030	0.132
PA	2006	Apr-Feb (M3)	1.071	1.134	0.971*	0.125
PB	All mating seasons	All mating	0.942	1.015	0.927*	0.132
PB	All birth seasons	All births	0.942	0.983	0.897*	0.120
PB	2004	Mar-Oct (M1)	0.942	1.052	0.960*	0.125
PB	2004-2005	Nov-Mar (B2)	0.942	0.958	0.875*	0.129
PB	2005	Apr-Aug (M2)	0.942	0.997	0.910*	0.126
PB	2005-2006	Sep-Jan (B3)	0.942	1.028	0.939*	0.108
PB	2006	Feb-Oct (M3)	0.942	1.008	0.920*	0.132
PB	2006	Nov- Dec (B4)	0.942	0.860	0.786*	0.120
PS	All mating seasons	All mating	0.580	1.008	1.217	0.212
PS	All birth seasons	All births	0.580	0.855	1.033	0.180
PS	2004	Mar-May (B1)	0.580	1.046	1.119	0.195
PS	2004	Jun- Sept (M1)	0.580	0.888	1.185	0.207
PS	2004-2005	Oct- May (B2)	0.580	0.962	0.960*	0.168
PS	2005	Jun- Sept (M2)	0.580	1.018	1.189	0.207
PS	2005-2006	Oct- May (B3)	0.580	0.825	1.087	0.190
PS	2006	Jun- Sept (M3)	0.580	1.021	1.328	0.232
PS	2006	Oct- Dec (B4)	0.580	0.934	0.981	0.171

*Range is not defensible ($D < 0.98$ or $M < .08$)

Table 2.8. Season 3 defensibility indices, calculated using seasonal range areas for each group. B = birth season, M = mating season.

Group	**Year(s)**	**Month(s)**	**Seasonal range area [km^2]**	**Day range length [km]**	**D**	**M**
PA	All mating seasons	All mating	1.154	1.152	0.951*	0.118
PA	All birth seasons	All births	0.883	1.011	0.954*	0.135
PA	2004	March (B1)	0.467	0.728	0.944*	0.184
PA	2004	Apr-Dec (M1)	0.849	1.183	1.137	0.164
PA	2005	Jan-Aug (B2)	0.889	1.004	0.944*	0.133
PA	2005-2006	Sept-Feb (M2)	0.998	1.116	0.990	0.132
PA	2006	March (B3)	0.852	1.203	1.156	0.166
PA	2006	Apr-Feb (M3)	1.151	1.134	0.937*	0.116
PB	All mating seasons	All mating	0.916	1.015	0.940*	0.131
PB	All birth seasons	All births	1.075	0.983	0.840*	0.108
PB	2004	Mar-Oct (M1)	0.832	1.052	1.022	0.149
PB	2004-2005	Nov-Mar (B2)	0.807	0.958	0.945*	0.140
PB	2005	Apr-Aug (M2)	0.965	0.997	0.899*	0.122
PB	2005-2006	Sep-Jan (B3)	1.173	1.028	0.841*	0.103
PB	2006	Feb-Oct (M3)	0.961	1.008	0.911*	0.124
PB	2006	Nov- Dec (B4)	0.895	0.860	0.806*	0.113
PS	All mating seasons	All mating	0.654	1.046	1.146	0.188
PS	All birth seasons	All births	0.508	0.888	1.104	0.206
PS	2004	Mar-May (B1)	0.344	0.962	1.453	0.329
PS	2004	Jun- Sept (M1)	0.579	1.018	1.186	0.207
PS	2004-2005	Oct- May (B2)	0.567	0.825	0.971*	0.172
PS	2005	Jun- Sept (M2)	0.442	1.021	1.361	0.272
PS	2005-2006	Oct- May (B3)	0.512	0.934	1.157	0.215
PS	2006	Jun- Sept (M3)	0.655	1.141	1.250	0.205
PS	2006	Oct- Dec (B4)	0.529	0.843	1.027	0.188

*Range is not defensible ($D < 0.98$ or $M < .08$)

Table 2.9. Percentage of *M* indices that are greater when calculated using seasonal home ranges than using complete home range.

	PA	**PB**	**PS**
All years and all seasons	68	32	66
Yearly	67	33	33
Season 1	67	33	67
Season 2	62	12	62
Season 3	88	50	78

Table 2.10. Percentage of *D* indices indicating the capacity for home range defense, calculated from both complete home range and seasonal ranges for each group.

Percentage of *D* indices ≥ 0.98	**PA**	**PB**	**PS**
All years and all seasons (complete home range)	31	3	83
All years and all seasons (seasonal range use)	38	10	97
Yearly (complete HR)	50	0	100
Yearly (seasonal range use)	25	33	100
Season 1 (complete HR)	33	11	67
Season 1 (seasonal range use)	33	11	100
Season 2 (complete HR)	13	0	88
Season 2 (seasonal range use)	50	0	100
Season 3 (complete HR)	38	0	89
Season 3 (seasonal range use)	38	13	89

Table 2.11. Colobine defensibility indices and territoriality (data from: Struhsaker 1975; Struhsaker and Leland 1987; Oates 1994; Podzuweit 1994; Koenig et al. 1997; Yeager and Kool 2000; van Schaik et al. 2002; Mukherjee, 2001). Where a species is listed more than once, multiple studies are shown.

Species	**Home range [ha]**	**Home range [km^2]**	**Daily path length [m]**	**Daily path length [km]**	**Home range diameter [km]**	**D**	**M[a]**	**Territoriality**
Colobus guereza	28	0.28	535	0.535	0.597	0.896**	0.075	Yes
Colobus polykomos	24	0.24	834	0.834	0.553	1.509	0.136	?
Colobus polykomos	48	0.48	307	0.307	0.782	0.393*	0.025*	?
Colobus satanas	60	0.60	459	0.459	0.874	0.525*	0.030*	?
Colobus satanas	84	0.84	510	0.51	1.034	0.493*	0.024*	?
Nasalis larvatus	130	1.30	706	0.706	1.287	0.549*	0.021*	No
Nasalis larvatus	900	9.0	800	0.8	3.385	0.236*	0.003*	No
Procolobus badius	70.7	0.707	648	0.648	0.949	0.683*	0.036*	No
Procolobus badius	9	0.09	603	0.603	0.339	1.781	0.263	No
Presbytis comata	38	0.38	500	0.5	0.696	0.719**	0.052**	Yes
Presbytis hosei	34.5	0.345	691	0.691	0.663	1.043	0.079	?
Presbytis hosei	44.8	0.448	794	0.794	0.755	1.051	0.070*	?
Presbytis melalophos	18.5	0.185	495	0.495	0.485	1.020	0.105	Yes
Presbytis melalophos	27.5	0.275	682	0.682	0.592	1.153	0.097	Yes
Presbytis melalophos	19.3	0.193	936 (?)	0.936	0.496	1.888	0.190	Yes
Presbytis melalophos	21	0.21	1150	1.15	0.517	2.224	0.215	Yes
Presbytis potenziani	34.3	0.343	540	0.54	0.661	0.817**	0.062**	Yes
Presbytis rubicunda	37.8	0.378	746	0.746	0.694	1.075	0.078	Yes
Presbytis rubicunda	84.8	0.848	890	0.89	1.039	0.857**	0.041**	Yes
Presbytis thomasi	14	0.14	684	0.684	0.422	1.620	0.192	?
Presbytis thomasi	37.7	0.377	1073	1.073	0.693	1.549	0.112	?
Rhinopithecus bieti	2525	25.25	1250	1.25	5.670	0.220*	0.002*	?
Rhinopithecus roxellana	2600	26.0	710	0.71	5.754	0.123*	0.001*	?

Species	**Home range [ha]**	**Home range [km^2]**	**Daily path length [m]**	**Daily path length [km]**	**Home range diameter [km]**	**D**	**M[a]**	**Territoriality**
Semnopithecus entellus	163	1.63	894	0.894	1.441	0.621*	0.022*	No
Semnopithecus entellus	74.5	0.745	1083	1.083	0.974	1.112	0.057**	Yes
Trachypithecus auratus	5.5	0.055	550	0.55	0.265	2.078	0.393	?
Trachypithecus cristatus	20	0.20	350	0.35	0.505	0.694**	0.069**	Yes
Trachypithecus francoisi	157	1.57	1000	1.0	1.441	0.707*	0.025*	?
Trachypithecus geei	2.5	0.025	300	0.3	0.178	1.681	0.471*	?
Trachypithecus geei	25	0.25	500	0.5	0.564	0.886*	0.079	?
Trachypithecus obscurus	33	0.33	559	0.559	0.648	0.862*	0.067*	?
Trachypithecus obscurus	28.5	0.285	950	0.95	0.602	1.577	0.131	?
Trachypithecus phayrei	27.5	0.275	500	0.5	0.592	0.845**	0.071**	Yes
Trachypithecus phayrei	95.8	0.958	1192	1.192	1.104	1.079	0.049**	Yes
Trachypithecus pileatus	21.6	0.216	324.5	0.325	0.524	0.620*	0.059*	No

[a] s = 50m (see Lowen and Dunbar 1994)

* = HR not defensible

**= HR not defensible, but species exhibits territorial behavior

References

Altmann, S.A. and Altmann, J. (1970). *Baboon Ecology*. University of Chicago Press, Chicago

Barrett, L. and Lowen, C.B. (1998). Random walks and the gas model: spacing behaviour of Grey-Cheeked Mangabeys. *Funct. Ecol.* 12: 857-865

Bartlett, T.Q. (2007). Seasonal home range use and defendability in white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. Abstract. 2007 AAPAs

Bartlett, T.Q. (2009). Chapter 13: Seasonal home range use and defendability in White-Handed Gibbons (*Hylobates lar)* in Khao Yai National Park, Thailand. In: *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*. Lappan, S. and Whittaker, D.J. (eds.) Springer, New York, pp. 265-275

Bennett, E.L. (1986). Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos*. *Folia Primatol*. 47: 26:38

Borries, C., Larney, E. Kreetiyutanont, K., Koenig, A. (2002). The diurnal primate community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, northeast Thailand. *Nat. Hist. Bull. Siam. Soc.* 50: 75-88

Borries, C., Larney, E., Derby, A.M., Koenig, A. . (2004). Temporary absence and dispersal in Phayre's Leaf Monkeys (*Trachypithecus phayrei)*. *Folia Primatol*. 75: 27-30

Brandon-Jones, D, Eudey, A.A., Geissmann, T., Groves, C.P., Melnick, D.J., Morales, J.C., Shekelle, M., and Stewart, C.B. (2004) Asian primate classifications. *Int. J. Primatol*. 25: 97-164.

Bronikowski, A.M. and Altmann, J. (1996). Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol*. 39: 11-25

Brown, J.L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bull*. 76:160-169.

Brown, J.L. (1982). Optimal group size in territorial animals. *J. Theor. Biol.* 95: 793-810

Brown, J. L. and Orians, G.H. (1970). Spacing patterns in mobile animals. *Ann. Rev. Ecol. System*. 1: 239-262

Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J Mammal*. 346- 352

Buzzard, P. J. (2006). Ranging patterns in relation to seasonality and frugivory among *Cercopithecus campbelli, C. petaurista* and *C. Diana* in the Taï Forest. *Int. J. Primatol.* 27: 559- 573

Charnoy. E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9: 129: 136

Cheney, D.L. (1987). Chapter 12: Interactions and relationships between groups. In *Primate Societies*. Smuts, B.B., Cheney, D.L., Seyfarth, R.M, Wrangham, R.W. and Strusaker, T.T. (*e*ds.). The University of Chicago Press, Chicago, pp 267-281

Chivers, D.J. (1969). On the daily behavior and spacing of howling monkey groups. *Folia Primatol.* 10: 48-102

Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In Clutton- Brock, T. H. (ed.) *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes.* Academic Press, New York, pp 539-556

Clutton-Brock, T. H. and Harvey, P.H. (1977). Primate ecology and social organization. *J Zool. London* 183: 1-39

Di Fiore, A. (2003a). Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *Am. J. Primatol.* 59: 47-66

Doran-Sheehy, D.M., Greer, D., Mongo, P.,Schwindt, P. (2004). Impact of social and ecological factors on ranging in Western gorillas. *Am. J. Primatol.* 64: 207-222

Emlen, S.T. and Oring, L.W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223

Fashing, P.J. (2001a). Activity and ranging patterns of guerezas in the Kakamega forest: intergroup variation and implications for intragroup feeding competition. *Int. J Primatol.* 22: 549- 577

Fashing, P. J. (2001b). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behav. Ecol. Sociobiol.* 50: 219-230

Fleagle, J. (1999). *Primate Adaptation and Evolution*. 2nd Ed. Elselvier. USA

Ganas, J. and Robbins, M.M. (2005). Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda a test of the ecological constraints model. *Behav. Ecol. Sociobiol.* 58: 277-288

Garber, P.A. (1993). Seasonal patterns of diet and ranging in two species of tamarin monkeys: Stability vs. variability. *Int. J. Primatol.* 14: 145-166

Gibson, L. and Koenig A. (in revision). Neighboring groups and habitat edges modulate range use in Phayre's leaf monkeys (*Trachypithecus phayrei*). *Behav. Ecol. Sociobiol.*

Goldsmith, M.L. (1999). Ecological constraints on the foraging effort of Western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Int. J. Primatol.* 20: 1-23

Grant, J.W.A., Chapman, C.A. and Richardson, K.S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behav. Ecol. Sociobiol.* 31: 149- 161

Groves, C.P. (2001). *Primate Taxonomy*. Smithsonian Institution Press. Washington D.C.

Hassel- Finnegan, H.M. Borries, C., Larney, E., Umponjan, M., and Koenig, A., (2008) How reliable are density estimates for diurnal primates. *Int. J. Primatol.* 29: 1175-1187

Harris, T. (2005). Roaring, intergroup aggression and feeding competition in black and white colobus monkeys (*Colobus guereza)* at Kanyawara, Kibale National Park, Uganda. Dissertation. Yale University.

Harris, T. (2007). Testing mate, resource and infant defense functions of intergroup aggression in non-human primates: issues and methodology. *Behaviour* 144: 1521-1535

Hooge, P.N. and Eichenlaub, B. (2000). Animal Movement extension to ArcView in. Alaska Science Center- Biological Sciences Office, US Geological Survey, Anchorage, AK.

Isbell, L.A. (1983). Daily ranging behaviour of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. *Folia. Primatol.* 35: 34-48

Janson, C.H. and van Schaik, C.P. (1988) Recognizing the many faces of primate food competition: methods. *Behaviour*. 105: 165-186

Jewell, P.A. (1966). The concept of home range in mammals. *Symposia Zoological Society of London* 18: 85-109

Kitchen, D.M., Cheney, D.L. and Seyfarth, R.M. (2004). Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*) *Behaviour*. 141: 197-218

Khon Kaen University and Phu Khieo Wildlife Sanctuary. (1995) *Integrated information system for the management of Phu Khieo Wildlife Sanctuary*. Khon Kaen University, Khon Kaen.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *Int. J. Primatol.* 23: 759-783

Koenig, A., Beise, J., Chalise, M.K., Ganzhorn, J.U. (1998). When females should contesst for food- testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*) *Behav. Ecol. Sociobiol.* 42: 225-237

Koenig, A., Larney, E., Lu, A., Borries, C. (2004a). Agonistic behavior and dominance relationships in female Phayre's leaf monkeys- preliminary results. *Am. J. Primatol.* 64: 351-357

Koenig, A., Borries, C. Suarez, S., Kreetiyutanont, K., Prabnasuk, J. (2004b). Socio-ecology of Phayre's leaf monkeys (*Trachypithecus phayrei*) at Phu Khieo Wildlife Sanctuary. *J. Wildlife in Thailand* 12: 150- 163

Kummer, H. (1995). *In Quest of the Sacred Baboon: a scientist's journey*. Princeton University Press, Princeton, New Jersey

Lincoln, R.J., Boxshall, G.A. and Clark, P.F. (1982). *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press

Lowen, C. and Dunbar, R.I.M. (1994). Territory size and defendability in primates. *Behav. Ecol. Sociobiol.* 35: 347- 354

Maher, C.R. and Lott, D. F. (1995). Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Anim. Behav.* 49: 1581- 1597

Mitani, J.C. and Rodman, P. S. (1979). Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav. Ecol. Sociobiol.* 5: 241-251

Newton, P. N. and Dunbar, R. I. M. (1994) Chapter 11: Colobine monkey society. In Oates, J. and Davies, G. (eds.) *Colobine Monkeys: their ecology, behavior and evolution*. CUNY Press, New York.

Noble, G.K. (1939). The role of dominance in the social life of birds. *The Auk* 56: 263-273

Pitelka, F.A. (1959). Numbers, breeding schedule and territoriality in pectoral sandpipers of northern Alaska. *The Condor* 61: 233

Raemakers, J.J. (1980). Causes of variation between months in distance traveled by gibbons. *Folia Primatol.* 34: 46-60

Roos, C. (2004). Molecular evolution and systematics of Vietnamese primates. In Nadler, T., Streicher, U. Ha, T.L. (eds.) *Conservation of primates in Vietnam.* Frankfurt: Frankfurt Zool Soc, pp 23-28

van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In Standen, V. and Foley, A. (eds.) *Comparative socioecology. The behavioural ecology of humans and other mammals.* Blackwell press, Oxford, pp 195-218

Snaith, T.V., and Chapman, C.A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Pilocolobus tephrosceles*). *Behav. Ecol. Sociobiol.* 59: 185-190

Stelzner, J.K. (1988). Thermal effects on movement patterns of yellow baboons. *Primates.* 29: 91-105

Struhsaker, T. (1974). Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *Am. Zool.* 14: 177-184

Sterck, E. H. M., Watts, D.P. and van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobio.* 41: 291-309

Trivers, R.L. (1972). Parental investment and sexual selection. In Campbell, B. (ed.) *Sexual selection and the descent of man, 1871- 1971.* Aldine Press, Chicago.

Waterman, P.G. and Kool, K.M. (1994). Colobine food selection and plant chemistry. In Davies, A.G., Oates, J.F. (eds.) *Colobine monkeys. Their ecology, behaviour and evolution.* Cambridge University Press, Cambridge. pp. 251-284

Waser, P.M. (1976). *Cercocebus albigena*: site attachment and intergroup spacing. *Am. Nat.* 110: 911-935

Wich, S.A. and Sterck, E. H. M. (2007). Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. *Behaviour.* 144: 1583- 1598

Wilson, M. L. (2007). Intergroup aggression in wild primates: Introduction. *Behaviour* 144: 1469- 1471

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75:262-300

Wrangham, R. W., Crofoot, M., Lundy, R. and Gilby, I. (2007). Use of overlap zones among group-living primates: a test of the risk hypothesis. *Behaviour* 144: 1599- 1619

Yeager, C.P. and Kool, K. (2000). The behavioral ecology of Asian colobines. In Whitehead, P.F. and Jolly, C. J. (eds.) *Old World Monkeys*. Cambridge University Press, Cambridge, pp 496-521