

Chapter 10

Social Organization and Male Residence Pattern in Phayre's Leaf Monkeys

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Abstract The genus *Trachypithecus* (Colobinae, Presbytini) has previously been characterized by one-male groups and both male and female dispersal. Occasionally, males may mature in their natal groups, resulting in so-called age-graded multi-male groups. Our long-term observations of a population of Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) in Thailand, while revealing values in group size and composition similar to other species, indicate a hitherto undescribed social organization, in which males mature and breed in their natal group or disperse and form new groups. Groups are not age-graded and multi-male groups are one phase of a dynamic social organization changing between multi-male and one-male constellations. The ways in which our views of the social organization of Phayre's leaf monkeys changed over a period of eight years underscore the importance of long-term studies for a full understanding of the behavioral ecology of long-lived species like primates.

10.1 Introduction

Until recently long-term studies on colobine monkeys, especially the tribe Presbytini (Asian colobines), were comparatively rare (see overview in Kirkpatrick 2007). Only two of the more than 50 species, in seven genera (Groves 2001), had been studied in detail, with multiple years of observation of identified individuals. These were Hanuman langurs (*Semnopithecus entellus*) at Jodhpur, India (e.g., Sommer and Rajpurohit 1989) and at Ramnagar, Nepal (e.g., Borries 2000), and Thomas langurs (*Presbytis thomasi*) at Ketambe, Indonesia (e.g., Steenbeek et al. 2000). This lack of long-term data is unfortunate, because the reliability of results from short-term studies is limited by default (Clutton-Brock and Sheldon 2010).

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Infrequent events will rarely be documented and life history traits and demographic data may be biased, which may lead to spurious results, especially in comparative studies (Borries et al. 2011). In addition, the two Asian colobines studied on a long-term basis have very different social systems. Hence, it is unclear what the range of social systems is among the Presbytini and whether anyone pattern predominates (for a recent classification attempt, see Grueter and van Schaik 2010). Lastly, the lack of long-term studies of Presbytini is unfortunate, because available data on group size and composition, the ecology of female social relationships, and the residence patterns appear not to fit “classic” socio-ecological explanations.

10.1.1 Asian Colobines: (Relatively) Unexplored and Enigmatic

Most genera of the Presbytini, including *Presbytis*, *Simias*, *Trachypithecus*, form comparatively small groups of 20 or fewer individuals (cf. Table 4 in Kirkpatrick 2007). Given the expectation that folivorous primates such as colobines experience little to no feeding competition and hence should face only weak constraints on group size (review in Snaith and Chapman 2007), the small groups in these taxa posed the so-called folivore paradox (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). The resolution of the paradox might be that the upper limit of group size depends not just on the trade-off between ecological costs (i.e., within-group scramble competition) and benefits (i.e., predation avoidance), but also on social constraints, particularly the risk of male takeover and infanticide (Crockett and Janson 2000). Specifically, if the rate of male takeover increases with female group size, the risk of infanticide may increase accordingly and limit maximum group size. Some evidence indeed supports this idea (Crockett and Janson 2000), but other explanations are plausible, either in addition or alternatively (Janson and Goldsmith 1995; Snaith and Chapman 2005, 2007). Thus, studies that unravel the constraints on group size in colobines, and in folivorous primates more generally, could also improve explanations of the folivore paradox.

Ecological models of female social relationships (e.g., van Schaik 1989) predict competitive regimes and female social structure reasonably well, but seem to be particularly weak in predicting dispersal patterns (Koenig 2002; Koenig and Borries 2009). Specifically, the models suggest that in female dispersal species contest competition and linear dominance hierarchies should be absent. However, in several such species females form linear dominance hierarchies and they may contest for food (e.g., mountain gorillas: Robbins et al. 2005; overview in Koenig et al. 2004). Hence, disclosing additional evidence for the links between feeding competition, social relationships, and female dispersal could improve the explanatory power of socio-ecological models.

The Presbytini also pose challenges for a comparative understanding of primate mating systems. The mating system of many nonhuman primates involves female defense polygyny, in which the number of adult males in bisexual groups is positively associated with the number of adult females and their overlap in

receptivity (Emlen and Oring 1977; Nunn 1999; Kappeler 2000). In these species, males usually leave their natal groups upon reaching maturity and aggressively take over or immigrate into other bisexual groups. Among the Presbytini, specifically the genera *Presbytis* and *Trachypithecus*, the situation is slightly more complicated. The mating system has been described as female defense polygyny (van Schaik et al. 1992) and groups usually contain relatively few females, which should make them easy for single males to defend (van Schaik and Hörstermann 1994). However, surprisingly often groups contain multiple males. At least for some populations, groups can be described as age-graded (*sensu* Eisenberg et al. 1972) with male tolerance allowing maturing males to stay (Sterck and van Hooff 2000). For unknown reasons the percentage of “true” multi-male groups and age-graded multi-male groups as well as male residence vary across Presbytini, and the costs and benefits of multi-male stages are poorly understood (Sterck and van Hooff 2000).

Exploring these three aspects of primate social systems requires investigating individual social strategies, reproductive decisions, and reproductive success of known individuals over multiple groups and years; thus, it requires a long-term approach.

10.1.2 Research Goals and Expectations

These questions on the constraints of group size, female feeding competition and dispersal, and the social organization and residence pattern of Asian colobines led us to search for an appropriate study species and site in 1998. The few published reports that were available at that time indicated that the genus *Trachypithecus* in general and the species *T. phayrei* in particular might be a good fit. This and other Southeast Asian species seemed to display group sizes (13–27 on average) intermediate between those of *Semnopithecus* (ca. 26 on average) and *Presbytis* (ca. 8 on average; based on Bennett and Davies 1994); the *Trachypithecus* values are close to a proposed switch point between strong and weak risk of infanticide and, conversely, between weak and strong feeding competition (see details in Crockett and Janson 2000). At the same time it seemed likely that females would disperse (Sterck 1998) and occasional multi-male groups of *T. phayrei* had been reported (Bennett and Davies 1994).

Following explorations in Northeast India and mainland Southeast Asia in 1998 and 1999, we settled on the Phu Khieo Wildlife Sanctuary (PKWS), Thailand, as study area and began to habituate the first group of *Trachypithecus phayrei crepusculus* in October 2000 (note that there is variation in nomenclature (*T. phayrei* vs *T. holotephreus*; Groves (2001) *contra* Brandon-Jones et al. (2004)) and uncertainty in subspecies/species assignment (*T. phayrei crepusculus* vs *T. crepusculus*; Groves (2001) *contra* Roos (2004); i.e., here we follow the nomenclature provided in Groves (2001)).

In the following, we will summarize main results of our study focusing on social organization and male residence pattern reporting how, over a period of 8 years,¹ our views changed. As in other Asian colobines, we expected male Phayre's leaf monkeys to exhibit female defense polygyny (van Schaik et al. 1992) with occasional age-graded multi-male groups (Sterck and van Hooff 2000). Because groups contain relatively few females and become multi-male due to tolerance and not due to changes in monopolization potential, we expected at most a weak positive relationship between the number of males and the number of females. In a strictly age-graded system, one would further predict that males remain in their natal groups for some time following maturation and that they can be ranked according to age (Eisenberg et al. 1972). We expected both sexes to disperse, but changes in male membership to occur primarily via male immigration and takeover (Sterck and van Hooff 2000). Alternatively, one might predict a true multi-male pattern with male immigration and takeover as in Hanuman langurs (Borries 2000), or a pattern in which groups form and disband through female dispersal as in Thomas langurs (Sterck 1997). However, even in Thomas langurs male takeovers have been observed occasionally (Steenbeek et al. 2000).

10.2 Field Site: History and Methods

10.2.1 Study Area and Site

The study area, PKWS, is located in Northeast Thailand (16°5'-35' N, 101°20'-55' E, Chaiyaphum Province, elevation: 300–1,300 m asl) and comprises an area of 157,300 ha as part of the Western Isaan Forest Complex, a conservation area of 598,400 ha in total (Kumsuk et al. 1999). The area became a wildlife sanctuary (the highest protection status in Thailand) in 1979 and is effectively protected via ranger patrols and helicopter surveys, although illegal logging, collection of aloewood (*Aquilaria crassna*), and poaching still occur occasionally (Grassman et al. 2005). The vegetation has been classified primarily as hill and dry evergreen forest (75%) in addition to some other plant communities (Grassman et al. 2005). PKWS harbors a diverse animal community that includes Asian elephant, Asiatic black bear, Malayan sun bear, Asian forest bison (gaur), and four deer species (Kumsuk et al. 1999). With eight out of the nine felids found in Thailand (e.g., tiger, leopard, clouded leopard, golden cat), two canids (jackal and dhole), ten viverrids, five larger raptor species, and two python species, the predator community is plentiful (Grassman et al. 2005).

¹ Systematic data collection ran from January 2001 to January 2009 when it was discontinued due to a lack of funding.

We selected a part of the dry evergreen forest at Huai Mai Sot Yai (16°27' N, 101°38' E; 600–800 m asl) as our study site for two reasons. First, the area is slightly hilly, but not too steep to follow arboreal primates. More importantly, cursory surveys indicated a relatively high diversity and density of primates. The primate community at Huai Mai Sot Yai consists of *T. phayrei* and *Hylobates lar*, three macaque species (*Macaca assamensis*, *M. leonina*, *M. mulatta*) and northern slow loris (*Nycticebus bengalensis*; Borries et al. 2002; Hassel-Finnegan et al. 2008).

The study site is accessible through a network of trails encompassing more than 100 km. Most of these trails were made by elephants and gaurs, with occasional connections cut between them. The trails were measured, marked, and GPS-mapped every 100 m. To put these data points on a map, we digitized the topographic maps of the area turning it into a digital elevation model.

10.2.2 Facilities

The presence of elephants did not allow maintaining a field camp close to the field site and facilities at the headquarters of the sanctuary could only be used for short periods of time. Hence, with support from the National Science Foundation we established a field station at the sanctuary's headquarters that consisted of a kitchen and lab, an office, and two residential buildings (four rooms each).

The disadvantage of this arrangement was a daily "commute" of 11 km (one way) on a small paved road to and from the headquarters located in the center of the sanctuary. However, the advantage of this arrangement was to have electricity (4 h a day via generator), which allowed running a freezer and other electrical gear (e.g., drying oven, mechanical food tester, computer, battery charging equipment, etc.). In addition, the size of the field station allowed the permanent presence of several assistants and students as well as smaller laboratory procedures and storage. Lastly, the location of the field station in the headquarters allowed researchers immediate contact with the sanctuary authorities, an important aspect for a smooth coordination of research activities. In addition, the headquarters has a helipad for emergency evacuation in case of accidents with elephants, gaurs, bears, or venomous snakes.

10.2.3 Data Collection

From the start, our project was designed as a long-term study with a multidisciplinary approach to primate behavioral ecology, particularly questions to group size constraints, the ecology of female social relationships, and female and male reproductive strategies. Accordingly, we collected data on primate community ecology along with data on the ecology, demography, life history, behavior, hormones, and genetics of Phayre's leaf monkeys. Our approaches and procedures

rested on published descriptions (see below) and our past field experience in India and Nepal. In addition, we profited from material and descriptions kindly made available by colleagues (e.g., unpublished monitoring guide by J. Altmann, S. Altmann, and G. Hausfater).

10.2.3.1 Ecological Data

Weather data that included temperature, humidity, and rainfall were recorded via data loggers. Temperature and humidity were recorded directly in the forest via two loggers (2 h intervals; one logger as a back-up). To measure rainfall, a flow-through rain gauge was set up ca. 6 km away from the study site at a ranger station. A rain gauge initially installed at the field site itself was destroyed by elephants after only a few months. A second rain gauge at the headquarters served as backup.

To estimate the forest composition and to measure plant distribution, we used a stratified random approach to establish 33 botanical plots, each 50 × 50 m; this represented ca. 3% of the home ranges of our study groups (Struhsaker 1975). Within each plot we measured all trees of ≥ 10 cm in diameter and all climbers of ≥ 5 cm in diameter (total of 4,538 stems). Botanical work was done primarily by the staff of the sanctuary, because in Thailand only forest personnel are permitted to collect plant parts (we requested and received a special permit for botanical work).

From the botanical plots we selected a subsample of trees and climbers for phenology data collection. We included as many plant species as possible, because in the beginning we did not know exactly, which species were langur food. The sample consisted of 546 trees and climbers from 121 species. If possible, we included 5–10 mature individuals per common species. Rare species ($N < 5$ in botanical plots) were included if the leaf monkeys were known to use them. Data for different phytophases were collected once a month in the middle of the month using a point scale (from 0 to 3) and a semiquantitative index based on \log_{10} (i.e., 0 for 1–9, 1 for 10–99 etc.; Janson and Chapman 1999). To circumvent problems with interobserver reliability, data were collected by two researchers.

10.2.3.2 Primate Community

To describe the primate community of the site, we conducted line transect sampling for four consecutive days each month on a 4-km transect. We discontinued the data collection after 480 km had been walked, when cumulative density analysis indicated no further improvement in data quality for the most common species (Borries et al. 2002; Hassel-Finnegan et al. 2008).

10.2.3.3 Habituation and Identification

We habituated four groups of Phayre's leaf monkeys. The area has experienced some hunting in the past, and all monkeys initially fled from observers. It took

several months to reliably count and identify all individuals, and habituation to the point when observers were ignored took 7–12 months per group.

The federal laws and regulations for research in forested areas in Thailand make it very hard to receive permission for capturing wild animals. Thus, to identify individuals we relied on traditional methods based on physical characteristics (National Research Council 1981). All group members were identified via the shape of their crest, eye rings, white muzzle, and the shape of depigmented skin below the belly button. We established an identification sheet for each individual and a library of digital images of the markers. These tools facilitated learning the identity of the monkeys within 1–2 months. Importantly, changes in physical characteristics required an annual update of the ID charts.

10.2.3.4 Demography and Life History

In general, we followed groups from dawn to dusk for a minimum of 4 days per month (mean: 8.7 days). During every follow, we completed at least one full group count and identified all members. We also recorded births, immigrations, disappearances, emigrations, injuries, and nipple contact. Once a month we assessed immature individuals to demarcate landmarks in growth by comparing their sitting height or head-body length to adult group members (National Research Council 1981). Individuals were considered juvenile if they were smaller than adult females. Subadult males were as tall as adult females, but smaller than adult males. Both males and females became adult, when they had reached the height/length of adult males or females, respectively. Once adult, individuals were assessed for several more months to assure that they had ceased growing. The demographic data allowed for compilations of weaning ages, interbirth intervals, and rates of maturation and dispersal. Altogether the study included 277 group-contact months and 23,677 contact hours (Borries et al. 2011).

Behavioral Data

Individual behavioral data were collected via 20 min focal animal sampling (Martin and Bateson 2007), in which we combined instantaneous sampling at 1-min intervals with continuous recording. Behavioral data emphasized feeding and social behavior of adults and, sometimes, juveniles. The length of a focal sample was determined based on the median time an observer could follow an individual monkey without interruption and the median duration of certain behavioral states such as grooming (E. Larney unpublished data). Agonistic and sexual behavior was also collected *ad libitum*. Depending on the research questions, these data were supplemented with data on grooming bouts, allomaternal care, feeding rates, nutritional data, food physical properties (Lucas et al. 2003), and other variables.

At the group level, we used scan sampling (Martin and Bateson 2007) at 30-min intervals to collect data on mutually exclusive activities (feeding, traveling, resting,

social) and on the height of individuals above the ground. We noted the behavior of all identified individuals except infants within 10 min. At the start and end of a group follow and on the hour and the half hour, we collected ranging data at the approximate geometric center of the group via a handheld GPS (UTM coordinates and error reading). We also collected group-level data on food patch depletion (focal tree samples; Snaith and Chapman 2005) and intergroup encounters.

10.2.3.5 Hormones and Genetics

We and our students collected fecal samples to investigate reproductive hormones (Lu 2009; Lu et al. 2010) and relatedness and paternity (Larney unpublished). Sample collection was noninvasive and followed standard procedures that either involved freezing (Lu et al. 2010) or a two-step ethanol-silica method (Nsubuga et al. 2004). As with botanical work, fecal sample collection required a special permit as well as CITES clearance for export.

10.2.3.6 Data Consistency

To ensure standardized data collection and interobserver reliability, we first established an ethogram for the species based on the behavioral repertoire for Hanuman langurs (Dolhinow 1978). The behavioral categories, including standard abbreviations and descriptions, were listed in a field manual that also explained all observational, sample collection, and data processing procedures and definitions. Such a manual is an essential tool in training and re-training of observers to ensure consistency in data collection over time. Consistency can be improved if training is conducted by the same individuals (in our study, ourselves and long-term rangers). In addition, we encouraged our assistants to specialize in certain tasks so that not everyone had to become an expert in all methods. Lastly, we conducted interobserver reliability tests (Martin and Bateson 2007) during training.

10.3 General Characteristics, Life History, and Social Organization

10.3.1 General Characteristics of Phayre's Leaf Monkeys

Phayre's leaf monkeys are midsized nonhuman primates. Adult individuals weigh about 6–8 kg with a moderate sexual size dimorphism, i.e., males weigh about 8 kg and females ca. 6–7 kg (Smith and Jungers 1997). Measurements, which we could take for one adult female (7.0 kg), confirmed the value for females.

Like many other Asian colobines, Phayre's leaf monkeys are primarily arboreal spending most of their time at heights between 5 and 50 m. During parts of the winter and spring (January–March), all groups come to the ground to eat soil and to drink. In October, they sometimes come to the ground to feed on bamboo shoots.

As members of the subfamily of Colobinae, Phayre's leaf monkeys are characterized by foregut fermentation (Bauchop and Martucci 1968) and with 46% of time feeding on leaves (data for adult individuals for three groups over 1 year; Borries et al. 2011) their diet fits the criterion for a folivorous primate (at least 40–45%; Leigh 1994). However, the amount of leaves is relatively small compared to other Asian colobines, which commonly have over 50% leaves in their diet (Kirkpatrick 2007). Conversely, Phayre's leaf monkeys devote a relatively high proportion of feeding time (35%) to fruits and seeds.

10.3.2 Life History

A recent compilation highlights similarities of life history traits of Phayre's leaf monkey with other wild Asian colobines (Lu et al. 2010; Borries et al. 2011). Female Phayre's leaf monkeys have their first infants at an average age of 5.3 years compared to 5.4 to 6.7 years for other Presbytini. The average duration of gestation is 205 days, in the middle of the range for other wild Asian colobines (198–212 days).

As in most other species of *Trachypithecus*, infants are born with a flamboyant natal coat (bright orange), which gradually changes to the adult gray coat over a period of 26 weeks (Borries et al. 2008; Larney and Koenig unpublished). Weaning (defined here as cessation of nipple contact) takes place at 19–21 months, and weaning age increases with group size (Borries et al. 2008). As in other colobines, Phayre's leaf monkey females nurse their infants almost until the next parturition (Borries et al. 2001, 2011). Thus, with an average of 22 months the interbirth interval following a surviving infant is only slightly longer than the mean weaning age (Borries et al. 2008). Interbirth intervals are significantly longer in larger groups. Because infant survival is independent of group size, these differences in reproductive rates may lead to differences across groups in mean female fitness.

These group size effects on reproductive rates stand in contrast to the absence of group size effects in folivorous mountain gorillas (Robbins et al. 2007) and are instead similar to those reported for frugivorous or omnivorous primates (van Noordwijk and van Schaik 1999; Altmann and Alberts 2003). In contrast to other folivores, increases in group size might have negative effects on reproduction in Phayre's leaf monkeys because much of their food comes from depletable patches (cf. Snaith and Chapman 2005, 2007). Alternatively or in addition, these group size effects may reflect co-variation of group size and habitat quality (Dunbar 1987; Harris and Chapman 2007).

10.3.3 Social Organization

In this population, Phayre's leaf monkeys formed bisexual groups averaging 19 individuals (Table 10.1). The mean sizes of our focal groups ranged from 12.1 to 25.7 individuals (range: 6–33), including means of 1.2–2.7 adult males (range: 1–5; Table 10.1). During one month the group PB had no adult male, because the single adult male was absent due to an injury. One-male and multi-male social organizations were about equally likely: in 48.4% ($N = 134$) of group-months, groups contained single adult males. The second (24.9%, $N = 69$) and third (15.9%, $N = 44$) most common constellations were two-male and three-male groups. Groups contained ca. 7 adult females on average; group means ranged from 4.3 to 10.4 (range: 3–12; Table 10.1). In most months (86.3%), the number of adult females ranged between four and ten. Groups typically contained close to 5 subadult or juvenile individuals and ca. 5.5 infants.

The size and composition of our focal groups varied considerably over the course of the study period (Table 10.1). Group size varied by a factor of 1.7 (PB) to a factor of 3.1 (PS) and female group size by a factor of 1.3 (PS) to a factor of 3.3 (PA). However, rather than a consistent direction of change, like the general increase in group size documented for muriquis (Strier and Mendes 2012), the changes in group size or female group size followed U, inverted U, J, or S shapes (results not shown). Only in group PA did total group size and the number of females increase overall during the study, although the increase was not steady. In addition to births and maturation, much of the variation was due to female dispersal (Borries et al. 2004). It took 16 months from the start of the study before the first female immigration could be documented; this apparently low rate was probably a habituation effect, given that we now know that female immigrations occurred at a rate of 2–3 per group-year.

These general characteristics of group size and female dispersal more or less matched our expectations: group size was indeed intermediate between *Semnopithecus* and *Presbytis* (cf. Kirkpatrick 2007), and, as in many other *Trachypithecus*

Table 10.1 Composition of the study groups until January 2009 (inclusively) arranged by group size

Group	Start	Adult males	Adult females	Subadults and juveniles	Infants	Group size
PS	Mar 2002	1.2 (1–2)	4.3 (3–7)	3.1 (0–7)	3.4 (1–5)	12.1 (6–19)
PA	Jan 2001	2.7 (1–4)	6.1 (3–10)	6.1 (3–9)	4.7 (1–9)	19.6 (14–27)
PO	Aug 2005	2.7 (1–5)	7.9 (7–9)	3.9 (1–6)	6.0 (3–8)	20.5 (15–26)
PB	Aug 2003	1.2 (0–3) ^a	10.4 (9–12)	5.6 (0–12)	8.6 (2–11)	25.7 (20–33)
Unweighted / weighted average		1.95 / 1.92	7.18 / 6.84	4.68 / 4.77	5.68 / 5.43	19.48 / 18.95

“Start” indicates the month of the first reliable demographic record. Mean values are given with ranges in parentheses. Results are based on 277 group-months totaling 2,405 contact days and 23,677 contact hours. For details on contact times see Borries et al. (2011)

^aOne month without an adult male; the only adult male had disappeared temporarily.

and *Presbytis* species (Sterck 1998), females regularly dispersed. However, compared to previous reports (Sterck and van Hooff 2000), the high frequency of multi-male groups (over 50%) was unexpected.

10.3.4 Female Group Size and the Number of Males

One-male groups were slightly smaller (17.57 ± 7.44 SD) than multi-male groups (20.22 ± 3.77 SD), but a mixed model ANOVA of group size per study year with “group identity” as random factor, hierarchically nested in social organization (fixed effect), showed no effect of the one-male *versus* the multi-male condition ($F = 0.19$, $p = 0.675$; Fig. 10.1a). Instead, “group identity” was the driving factor ($F = 136.58$, $p < 0.001$). The number of females in one-male groups was marginally higher (6.95 ± 2.98 SD) than the number in multi-male groups (6.73 ± 2.15 SD). Again, a mixed model ANOVA showed no effect of the one-male *versus* the multi-male condition ($F = 0.01$, $p = 0.937$), while the random factor “group identity” had a significant effect ($F = 150.93$, $p < 0.001$). Only for group PS did the number of females differ significantly between the one-male and the multi-male stage, with more females present when the group had multiple males (Fig. 10.1a).

The socio-ecological model (Emlen and Oring 1977) predicts that the number of males per group is positively related to the number of females. However, monthly data from 276 group-months (excluding one month with no adult male in PB) gave only a weak positive association between the number of females and the number of males (Pearson's $r = 0.117$, $p = 0.052$; Fig. 10.1b) that explained less than 2% of the variance. The number of males was much better predicted by a quadratic fit in the form of an inverted U-shape: it initially increased with the number of females,

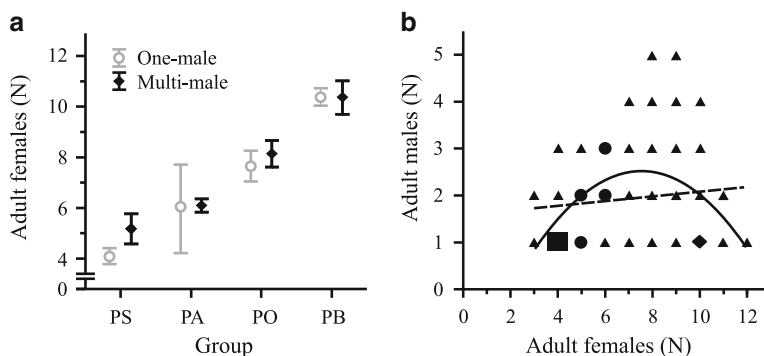


Fig. 10.1 Relationship between the number of adult females and males. (a) Number of adult females per group in relation to social organization (one-male *vs* multi-male) of the four focal groups. Group size increasing from left to right. Mean values and 95% confidence limits are given. (b) Number of males in relation to the number of females. Size and style of markers indicate the number of group-months (*triangle*: 1–10, *circle*: 11–20, *diamond*: 21–30, *square*: >40). Linear fit (*hatched line*): $y = 1.58 + 0.05x$; quadratic fit (*solid line*): $y = 0.41 + 0.11x + 0.01x^2$

but then decreased (similar shapes were found for fitted functions such as Lowess or Weighted Least Squares).

Overall, these results indicate that the number of males was not strongly affected by the monopolization potential of females, contrary to the socio-ecological model (Emlen and Oring 1977) and to results from Nunn's (1999) comparative analysis of data from many primate species. Instead the results were similar to other *Trachypithecus* species (Sterck and van Hooft 2000), in which multi-male groups are primarily age-graded.

10.4 Male Residence Pattern and Group Dynamics: Benefits of a Long-Term Approach

While data on group composition can answer questions on social organization and interrelationships between the number of males and females, they cannot answer questions about stability and age-gradedness of multi-male constellations. How do groups form and how are multi-male groups (or one-male groups) maintained? Do males immigrate and/or take over groups? Do they form new groups? Are males tolerated beyond maturation? Particularly questions that relate to rare events as well as to stability and maturation can only be answered with long-term data. In the following, we will therefore describe male residence patterns and group dynamics in our study population.

10.4.1 Male Residence Pattern: The First 5 Years

We started habituating the first study group (PA) in October 2000. PA's home range (bold outline; Fig. 10.2) was surrounded by those of five other bisexual groups (gray outline; Fig. 10.2). At least one of these groups (to the northeast) was a multi-male group, although its exact composition was unknown. Also, in the southeast of PA we occasionally encountered adult or nonadult males, who might have belonged to an all-male band. As of January 2001, PA itself had seven adult females with offspring. It also contained one adult and two subadult males – one bigger, one smaller – and thus had the potential to turn into an age-graded group. However, we did not know whether the oldest male was the father of the younger males and whether the males were natal. In 2002, the all-male band in the southeast of PA became a bisexual group (called R), but it was not clear, how this group had formed. Also, the group to the northeast of PA seemed to have fissioned into a small easily recognizable group with one adult male (group L) and a second group, farther to the northeast, with several males and females. During this year, male membership in PA remained stable and we habituated the second study group, PS. In the following 3 years (2003–2005) we habituated two more groups, PB and PO.

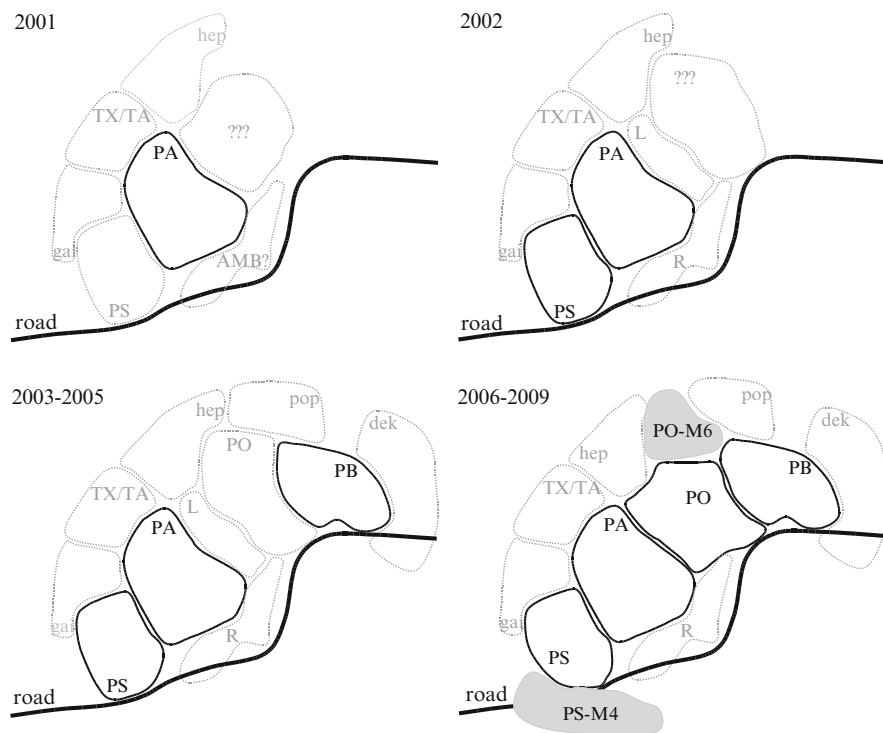


Fig. 10.2 Approximate location of home ranges of the study groups (*bold outline*) and their neighbors (*gray outline*) during the course of the study. Minor shifts of home ranges and their generally small overlap are not shown for simplicity. *Gray areas* indicate two new groups formed in 2008 by males from PO and PS (details see text)

In our four focal groups, male membership remained rather stable over the first 5 years of study. Four natal juvenile males (two in PA, two in PB) and one adult male from PA, who had matured in that group, disappeared (Table 10.2). In addition, one subadult natal male in group PA was twice temporarily absent. The absences of the subadult male were triggered by fights among the males. In the end, however, he returned to his natal group and, when adult, became the alpha male.

Thus, over the first 5 years of our study (133 group-months) not much happened with regard to male dispersal. We neither witnessed male takeover nor male immigration except as a return of a natal male. Because we had regularly witnessed female immigrations, this absence of male immigrations was presumably not caused by a lack of habituation. The question of age-gradedness was hard to answer, because only two males (one natal and one potentially natal) had matured and stayed. However, their continued residence was not a result of male tolerance as suggested for an age-graded structure. Maturing males had frequent, occasionally severe fights (Fig. 10.3) with each other or with older males (one older male lost an

Table 10.2 Disappearances and dispersal of males between January 2001 and January 2009

Years	Event	Age classes		
		Juvenile	Subadult	Adult
2001–2005 (133 group-months)	Disappearance	4		1
	Temporary absence		2	
2006–2009 (144 group-months)	Disappearance	5	1	2
	Temporary absence		2	4
	Emigration ^a	2	1	5
	Group fusion ^b			1

For each male all events were included, i.e., some males contributed more than once to the dataset. Emigration indicates that males had been relocated after they had left their group. Temporary absence indicates that males had been seen outside their group, but that they returned after a mean absence of 34 days (range: 2–90 days)

^aAll eight events refer to the formation of two new groups (see text for details)

^bThe small nonstudy group L (1 adult male, 1 adult female, 1 juvenile female) fused with group PO, from which it had likely fissioned several years earlier

Fig. 10.3 A subadult male from PS after a severe fight with the only adult male in the group, in which his right shoulder and neck were severely wounded. When adult, he challenged the male again and became the alpha male. Several months later the former alpha male left with three immature males and formed a new group (cf. Fig. 10.2). Photo © Andreas Koenig



eye). The timing of male rank ascendance always coincided with males reaching adulthood and was likely related to a power shift between maturing and aging males. The presence of peers seemed not to have influenced rank ascendance. If anything, fights among maturing males might have prevented or delayed ascendance. In general, contrary to our expectations and instead similar to Ugandan red colobus monkeys (*Piliocolobus tephrosceles*; Struhsaker 2010), males seemed to be philopatric. As in red colobus monkey, males occasionally emigrated from their natal groups, sometimes only temporarily, but unlike in red colobus we had not seen immigrations and group dissolution.

10.4.2 Male Residence Pattern: The Next 3 Years

In the following years (2006 to January 2009; 144 group-months), most male membership changes fitted the pattern described earlier: several juvenile, subadult, and adult males disappeared or were temporarily absent (Table 10.2). Temporary absences often occurred in connection with fights among group males. In addition, group L (1 adult male, 1 adult female, 1 juvenile female), which was sandwiched between groups PA and PO, fused with PO and its male became a member of PO (Fig. 10.2). While this event technically represented an “immigration” by an adult male, it resulted from a group fusion, during which the male returned to his original group. Given our previous observation we presume that the groups split in 2002 (or the male left and formed a new group; see below) and 4 years later the groups fused again. It seems noteworthy that none of the infants born in the small group L survived.

Events observed in the following years would change our perception of the male residence pattern further. In 2007, four of the five adult males of PO left (Table 10.2). Again this happened after severe fights. In contrast to other cases, in which males disappeared from the area, we encountered these four males occasionally at the periphery of the home range of PO. In 2008, the males had been joined by females, forming a new group north of PO (called PO-M6; Fig. 10.2). Because we did not follow this group regularly (all females were unknown to us and unhabituated), it is not entirely clear whether and how much area PO or other groups “lost” in the process of group formation. Importantly, some of the females in this new group had relatively old infants with adult coats, indicating that these infants had been born prior to group formation. Thus, females with infants must have joined the males. Some months later, an adult male (M4), plus a subadult and two juvenile males left group PS and moved south, leaving PS with a single natal adult male (Fig. 10.2; Table 10.2). These four males were joined by females with older infants, forming a new group (PS-M4). As in the case of PO, none of the females was from the males’ former group.

These events, which happened after more than 7 years of study, showed clearly that some males manage to form new groups, while others emigrate but eventually return to their natal group. Thus, males have more reproductive options than breeding in their natal group. Interestingly, both mass emigrations of males seemed unrelated to male rank ascendance, but took place after the mating season and the new groups were established before the beginning of the next mating season. Since most females in their old group were pregnant and would not conceive in the next mating season, emigration and group formation might have been the result of poor reproductive prospects. Why infanticide did not occur in the context of group formation (Sterck et al. 2005) remains an open question.

Importantly, based on our initial observations one would have concluded that the adult males within a group were more or less closely related to each other (depending on group size, reproductive skew, and extra-group paternity; Lukas et al. 2005). However, during group formation, males were joined by females with

infants, indicating that males co-residing in these groups may not be related at all. How extensively relatedness among group males varies is a question we hope to answer with the analysis of DNA samples. In any case, the residence pattern emerging from these observations also helped us to better understand the variable social organization of groups.

10.4.3 Group Dynamics and Group Life Cycle

One aspect of social organization, i.e., the number of adult males in our study groups, varied considerably through time (Fig. 10.4). Some of the groups had extended periods with only a single adult male, while others contained multiple males for extended periods. In all groups, this variation arose solely through male emigration or disappearance and maturation.

In PS, one adult male was present most of the time until one of the natal males matured in 2007. This natal male eventually became the alpha male, and later the only male, when in 2008 the former alpha male and 3 younger males left to form a new group (see above). Thus, the group switched from one-male to multi-male, then back to one-male. In PA, the number of adult males varied between one and four; it gradually increased during the study, and the group was multi-male 98% of the time. Changes in the number of adult males occurred through occasional

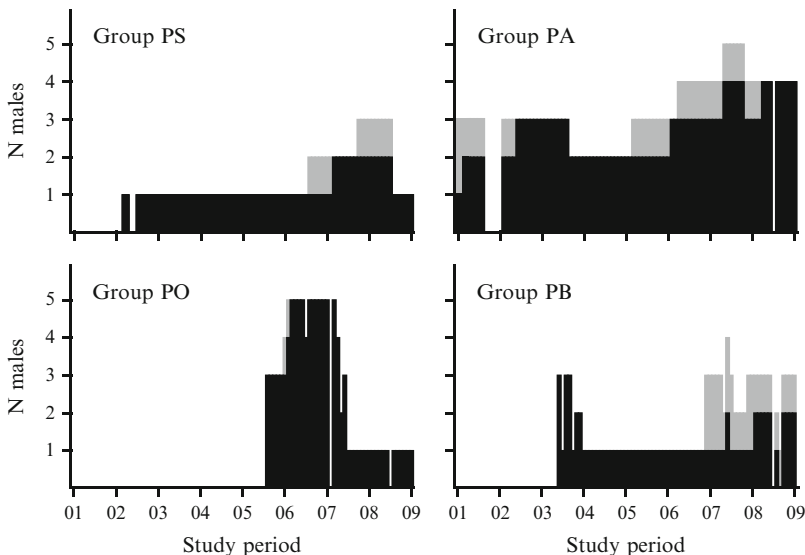


Fig. 10.4 Number of adult and subadult males of the four study groups over the study period 2001–2009. With one exception (see text) changes did not occur through immigrations but through maturation of natal males and emigrations/disappearances. *Black bars*: adult males; *gray bars*: subadult males; no column = no data available (except for group PB in September 2008 when the only adult male disappeared temporarily)

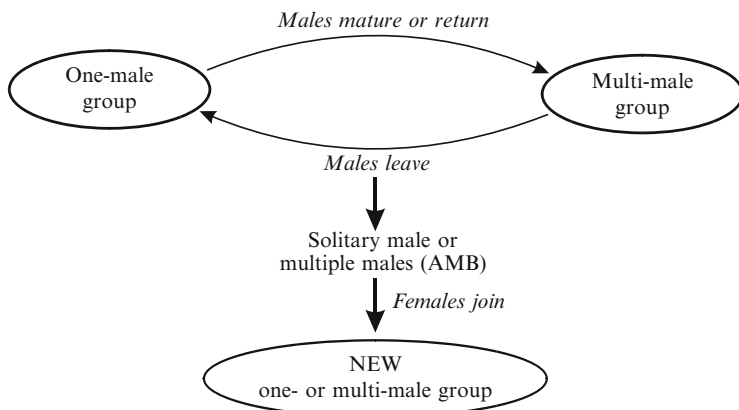


Fig. 10.5 Life cycle of Phayre's leaf monkey groups

disappearances and through maturation of natal males. When our observation of PO started, the group had multiple males. Four of these males left and formed a new group, and PO became one-male. Lastly, PB was initially a multi-male group. However, after adult males disappeared, it was one-male until natal males matured and it turned multi-male. Unfortunately, in this group the adult male died (likely due to predation by a clouded leopard or a leopard) right at the time when the first natal males matured. Thus, we do not know whether one of the maturing males would have overthrown the old male to become the new alpha male.

In essence, it seems that groups follow a rather simple “life cycle” (Fig. 10.5). Groups may change between a one-male and a multi-male stage either when males mature and breed in their natal group or when maturing natal males emigrate, either permanently or temporarily. In the latter process a group may or may not become one-male, depending on the number of males leaving a multi-male group. Dispersing males may either form new one-male or new multi-male groups. In contrast to other Asian colobines (Sterck and van Hooff 2000), we have never witnessed a takeover by a strange male or immigrations of males that were not natal (or likely natal). Similarly, in contrast to other long-term studies we have not seen groups dissolve through female dispersal (Sterck 1997). While we cannot be entirely sure that takeover, immigrations, or group dissolution will never happen, after 277 group-months we can be reasonably sure that they will be rare.

The emerging picture of the social organization of Phayre's leaf monkeys and the “life cycle” of a group is reminiscent of group dynamics in mountain gorillas (Watts 2000; Robbins 2007). Mountain gorillas are similarly characterized by natal and secondary dispersal of females and conditional male dispersal. While some groups have been found to be age-graded, in other cases natal males may become dominant over (presumed) fathers and brothers. However, unlike the nonterritorial female defense polygyny system of mountain gorillas, male Phayre's leaf monkeys actively defend areas with little overlap between groups, i.e., they defend territories (Gibson and Koenig unpublished). This pattern is more consistent with the resource

defense polygyny system of chimpanzees (Williams et al. 2004). In the end, male reproductive strategies in Phayre's leaf monkeys might possibly best be described as a mixture of gorilla and chimpanzee strategies.

10.5 Conclusions

The ways in which our views have changed through time emphasize the tentative nature of short-term studies and the importance of long-term studies for a full understanding of the behavioral ecology of long-lived species like primates.

Overall, group size and composition in Phayre's leaf monkeys were similar to other species of the genus *Trachypithecus* (Sterck and van Hooff 2000). However, only our long-term results revealed a social organization differing from other Asian colobines in several aspects: unlike the "true" multi-male groups described for Hanuman langurs, variation in the number of males was not affected by the number of females and one-male groups did not turn into multi-male groups *via* immigrations (Borries 2000). But Phayre's leaf monkeys also did not resemble the one-male structure with occasional age-graded groups of Thomas langurs, in which the multi-male phase may be a transitional stage after sons have matured and before a group dissolves or is taken over (Steenbeek et al. 2000). In Phayre's leaf monkeys, males may breed in their natal groups or they may disperse and form new groups. Even adult (breeding) males may disperse to form new groups. Multi-male groups were a regular part of a dynamic system that changed back and forth between a multi-male and a one-male stage with the occasional formation of new groups. Unlike species such as Thomas langurs (Steenbeek et al. 2000), however, multi-male stages were not age-graded (Eisenberg et al. 1972). Rather, dominance rank in relation to age followed an inverted U-shape, indicating that dominance rank depends on male resource holding potential as in baboons (Packer 1979).

Grueter and van Schaik (2010) recently proposed three main categories of social organization for Presbytini: (1) one-male groups with male immigrations (with occasional age-graded multi-male groups; most *Presbytis* spp., *Trachypithecus* spp.), (2) "true" multi-male groups with male immigrations (with a variable proportion of one-male groups; *Semnopithecus* spp.), and (3) multi-level societies (most snub-nosed monkeys). This scheme must now be expanded to include a fourth form of social organization: one- and multi-male groups with male philopatry and new group formation (*T. phayrei crepusculus*). Given the fragmentary and short-term nature of data for most Asian colobines, it is possible that the social organization described here is not unique. For example, multi-male groups have consistently been found in red-shanked Douc langurs (Lippold and Vu 2008). Given that male dispersal might be conditional, depending on the costs of dispersal and breeding opportunities in multi-male groups (Watts 2000), the possibility exists that these groups resemble the pattern of Phayre's leaf monkeys. Only increased efforts to conduct more long-term studies with Asian colobines could offer an answer.

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