POSITIONAL BEHAVIOR AND SUPPORT USE OF THE TONKIN SNUB-NOSED MONKEYS (*RHINOPITHECUS AVUNCULUS*) IN KHAU CA FOREST, HA GIANG PROVINCE, VIETNAM

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Le Khac Quyet (Ph.D., Anthropology)

Positional Behavior and Support Use of the Tonkin Snub-nosed Monkeys (*Rhinopithecus avunculus*) in Khau Ca Forest, Ha Giang Province, Vietnam

Thesis directed by Professor Herbert H. Covert

Studies of the positional behavior of wild primates are important for understanding relationships between ecology, behavior and morphology. The aim of this study was to examine the effects of body size, dimorphism, ontogeny and seasonal changes on positional behavior and support use of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*). From January 2009 to December 2010, I collected videography-based data on the positional behavior and support use via bout sampling method of *R. avunculus* in Khau Ca Forest, Ha Giang Province, Vietnam. I also studied the forest structure and phenology of the habitats of *R. avunculus* in Khau Ca Forest. Using G-tests (Row x Column statistical comparisons), I tested for significant differences in postural and locomotor profiles for associated maintenance activities, sex- and age-based differences, and seasonal changes for the Tonkin snub-nosed monkeys.

First, I documented the positional repertoire of adult male *R. avunculus* to include nine locomotor modes (19 submodes) and six postural modes (16 submodes). Quadrupedalism was the most frequent locomotion, followed by leap, climb, drop, arm-swing, and other locomotion. Sitting was the most frequent posture, followed by stand, lie, cling and other postures.

Second, I tested sex-based differences in positional behavior and support use of *R. avunculus*. The results showed that there were differences between adult males and females in positional behavior and support use, but these differences did not consistently follow the predictions based on body size.

Third, I found there were significant age-based differences in positional behavior and support use of *R. avunculus* during maintenance activities. Larger-bodied adults climbed more frequently, and leapt less frequently than smaller-bodied juveniles and infants during travel. The frequency of sitting increased with age while resting and feeding. Larger-bodied adults tended to use larger supports and more flexible supports than smaller-bodied juveniles and infants.

Finally, the data indicated that there were significant differences between dry/cold and wet/warm seasons in positional behavior and support use of *R. avunculus*. Seasonal changes in positional behavior and support use of *R. avunculus* might be associated with the shift of diet, foraging/feeding behavior, and ambient temperatures by seasons.

To Le Khac Que and Tran Thi Huyen, my parents

Nguyen Thi Thanh Binh, my wife

and

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CHAPTER I

INTRODUCTION

1.1. General Introduction

Garber (2011, p. 548) noted that studies of primate positional behavior are "central to an understanding of primate adaptive diversity because major changes in the ability of primate linages to exploit their environment are associated with evolutionary changes in positional behavior and positional morphology". Studies of the positional behavior of primates in the wild are significant for understanding relationships between ecology, behavior and morphology of living primates, and reconstructing the behavior of other extinct primates as well (e.g., Dagosto and Gebo, 1998; Fleagle, 1999; Kinzey, 1967; Schmitt, 2003). In terms of conservation, studies of positional behavior and support use can provide a comprehensive assessment of primate population health in relationship to habitat structure changes, as well as be of benefit for preparing suitable habitat for primates in zoos, reintroduction programs, and habitat expansion and rehabilitation projects (Aronsen, 2004; Cheyne, 2011).

The Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) is listed as critically endangered (IUCN, 2013), is restricted to small, forested areas in northeastern Vietnam, and is one of the 25 most endangered primates in the world (Mittermeier *et al.*, 2012). To date, there have been relatively few field studies of *R. avunculus*. The literature on this species consists primarily of information on social organization and behavior, feeding ecology, ranging behavior, and conservation needs (e.g., Boonratana and Le Xuan Canh, 1998; Covert *et al.*, 2008; Dong Thanh Hai, 2011; Le Khac Quyet and Covert, 2010; Le Khac Quyet *et al.*, 2007; Nguyen Thi Lan Anh *et al.*, 2011; Nguyen Thi Lan Anh *et al.*, 2007; Pham Nhat, 1993, 1994). Although these studies have provided preliminary data documenting general aspects of *R. avunculus* behavior and ecology, detailed research on the positional behavior of *R. avunculus* has yet to be undertaken. The aim of this study was to document the positional behavior repertoire of *R. avunculus* and to examine relationships among positional behavior and support use, body size, ontogeny, and seasonal changes for *R. avunculus* in the Khau Ca Forest, Ha Giang Province, Vietnam. This involved analyses to test hypotheses regarding associations between *R. avunculus*' positional behavior and body size, sex-based and age-based differences, substrate preference, and seasonal cycles. The significance of this study to anthropology includes expanding our knowledge of *R. avunculus*, the genus *Rhinopithecus*, and more generally, Asian colobine behavioral ecology.

1.2. Research Questions and Hypotheses

Field studies on positional behavior of nonhuman primates have usually focused on association of positional behavior and morphology (e.g., Fleagle, 1976a, 1976b, 1977, 1978; Ward and Sussman, 1979; Wright, 2005, 2007), body size (e.g., Doran, 1993; Fleagle and Mittermeier, 1980; Sugardjito and Vanhooff, 1986), ontogenetic development (e.g., Bezanson, 2006a, 2006b, 2009; Biondi *et al.*, 2011; Crompton, 1983; Rose, 1977; Wright, 2005), and a wide variety of ecological factors including support size (e.g., McGraw, 1998a, 1998b; Morbeck, 1977), diet (e.g., Garber, 1980, 1984), habitat structure (e.g., Garber, 1984; Morbeck, 1977; Rose, 1977), seasonality, and interspecific competition (e.g., Dagosto, 1995; Mittermeier, 1978). This study addresses four primary research questions and based on information from the research cited above along with other studies of primate positional behavior I offer hypotheses for each of the research questions:

1) **What are the defining and unique characteristics of *R. avunculus*' positional behavior? How do *R. avunculus* utilize the available substrates within their habitat at Khau Ca?** Following McGraw (1998a) observations that larger colobines leap more frequently than smaller colobines I propose that leaping will be frequent given the large body size of this species, I expect its locomotor repertoire should include higher frequencies of leaping and suspensory

behaviors and climbing, and lower frequencies of running and walking. I expect its postural repertoire would include higher frequencies of sitting, reclining and quadrupedal standing, and lower frequencies of bipedal stand and cling. I expect that *R. avunculus* would more frequently use large-sized substrates and less frequently use small-sized substrate in locomotor and postural behaviors.

2) **Do male and female *R. avunculus* differ in the frequencies of locomotor and postural behaviors and support use in Khau Ca Forest?** Because of high sexual dimorphism, I expected that there would be sex-based differences in the locomotion, posture, and substrate use of *R. avunculus*, such that larger-bodied adult males will more frequently use suspensory behavior and less frequently leap than smaller-bodied adult females (*sensu* McGraw, 1998a). Males would more frequently use sitting and standing behaviors, and less frequently bipedal stand and cling.

3) **What are the ontogenetic patterns of positional behavior of *Rhinopithecus avunculus* across different associated maintenance activities? Do age-related differences in body size influence positional behavior and substrate use? When do adult patterns of positional behavior appear during ontogeny in *Rhinopithecus avunculus*?** Ontogenetically, I expected that there would be age-based differences in the locomotion, posture, and substrate use of *R. avunculus*. Larger-bodied adults will more frequently use suspensory behaviors and less frequently leap, compared to smaller-bodied immature individuals. Adults would more frequently use sitting and standing behaviors and less frequently bipedal stand and cling. Adults would use larger substrates more commonly than immature individuals, and while foraging on smaller substrates adults would more commonly use suspensory postures than immature individuals.

4) **Is there any seasonal variation in positional behavior, and if so, which locomotor and postural behaviors are most affected?** Inhabiting a seasonal forest in Khau Ca area, I expected there would be differences in the positional behavior and substrate use by *R. avunculus* associated with seasonal (i.e., warm/wet versus cold/dry) changes: *R. avunculus* would more

frequently use leaping and suspensory behaviors, and smaller substrates in warm/wet season, and more frequent use sitting, and larger substrates in cold/dry season.

1.3. Research Significance

The significance of this study is three-fold. First, the results of this study provide, for the first time, data about *R. avunculus*' positional repertoire, and relationships between positional behavior and body size, sex- based and age-based differences, substrate preferences, and seasonal changes. This study provides a systematic investigation of positional behavior and support use of *R. avunculus*. Ideally, data on positional behavior would have been collected on identified individuals over a consistent time frame. Unfortunately, this was not possible. While the Tonkin snub-nosed monkeys at the study site of Khau Ca Forest of Ha Giang Province are only semi-habituated (the do not immediately flee when contacted, for example), we have not been able to identify individuals due to the complexity of the terrain requiring most observations to be made from some distance.

Second, this study is at the interface of conservation biology and anthropology as described by Borgerhoff-Mulder and Coppolillo (2005). Of particular importance, this study has encouraged local people to become involved in conservation activities in Khau Ca area in a variety of ways including providing employment such as local research assistants. During this fieldwork, I had the good fortune of working with local people who have provided a great deal of help, especially my local research assistants who provided both excellent assistance in the field and great friendship.

Finally, this study addresses a number of questions surrounding primate evolution, ecology, and conservation. The data on positional behavior and support use of *R. avunculus* from this study contributes to our understanding of the natural history and adaptations of this primate endemic to Vietnam as well as other Asian colobines and fossil primate species. In addition, with these data we can begin to evaluate suggested similarities and differences that have been noted about African and Asian colobines and add to our understanding of the evolutionary history of these primates. For example, it has been argued that *R. avunculus* closely resembles the primitive condition for snub-nosed monkeys (e.g., Jablonski, 1995; Jablonski and Peng, 1993; Liedigk *et al.*, 2012; Wang *et al.*, 2012), thus data on this species could provide insights into the locomotor pattern of fossil monkeys such as *Mesopithecus* and some of the stem apes including *Proconsul* (e.g., Jablonski, 2002; Pan *et al.*, 2004; Youlatos and Koufos, 2010; Zhao and He, 2005).

1.4. Outline of Dissertation

Following this introduction, Chapter II provides a general overview of primate positional behavior, a brief natural history of the odd-nosed monkeys, general information on the behavioral ecology of *R. avunculus*, and primate conservation in Vietnam. Chapter III provides information on the study site, research subjects, and general methods that were used for data collection and analysis throughout this study and brief information on statistical tests used as well. In Chapter IV, the forest structure of Khau Ca Forest is described, as well as the habitat's annual phenological and weather patterns. Chapters V, VI, VII, and VIII are the main data chapters and as such they are structured differently from the previous chapters. Chapter V presents positional repertoire and support use of adult male *R. avunculus* with comparisons to other African and Asian colobines. In Chapter VI, the differences between adult male and adult female *R. avunculus* in positional behavior and support use are described and compared with previously studied primates. In Chapter VII, age-based differences in *R. avunculus*' positional behavior and support use are described. In Chapter VIII, the influences of seasonal changes in *R. avunculus*' positional behavior and support use are described. Finally, in Chapter IX, the findings are summarized and the conclusions reached in this dissertation are reviewed. How the data in this study impact current understanding on the natural history of odd-nosed monkeys generally and Tonkin snub-nosed monkeys specifically is discussed.

CHAPTER II

BACKGROUND

2.1. Introduction

This chapter provides background information for my study. First, I provide a general overview of primate positional behavior, followed by a brief examination of the natural history of odd-nosed monkeys, with more specific information on the behavioral ecology of my study species, the Tonkin snub-nosed monkey (*R. avunculus*). Lastly, I address primate conservation in Vietnam.

2.2. Primate Positional Behavior

2.2.1. Brief History

The study of positional behavior was precisely defined by Prost (1965:1202) as “the study of how and when an animal establishes particular spatial relations between his body mass and his physical environment.” Positional behavior encompasses both locomotor and postural behaviors. Prost’s definition has been applied to primate positional behavior studies by various researchers, e.g., Aronsen (2004), Bitty and McGraw (2007), Blanchard (2007), Cant (1987, 1988), Chatani (2003), Crompton (1986), Dagosto (1995), Dagosto and Yamashita (1998), Doran (1992a, 1993), Fleagle (1977), Fleagle and Mittermeier (1980), Garber and Pruetz (1995), Hunt (1991), Isler and Gruter (2006), Lawler (2006), Lawler *et al.* (2006), Manduell *et al.* (2011), McGraw (1996a, 1998a, 1998b, 2000), Mittermeier (1978), Mittermeier and Fleagle (1976), Morbeck (1977), Off and Gebo (2005), Remis (1995), Stafford *et al.* (2003), Susman *et al.* (1980), Thorpe and Crompton (2005, 2006), Workman and Schmitt (2012), and Wright (2005, 2007).

Ripley's research on gray langurs (*Semnopithecus* [*Presbytis*] *entellus thersites*) in Ceylon (now Sri Lanka) is sometimes described as the first field study of primate positional behavior. Results of this study were presented in the 1965 symposium and demonstrated the need for detailed locomotor behavior analyses to substantiate the relationship between morphology and behavior (Ripley, 1967).

A symposium of particular historical relevance was held in September of 1965 at the University of California where researchers/participants discussed theory and methods related to primate locomotion studies (Kinzey, 1967). The outcomes of this symposium proved to be a powerful impetus for a number of ground breaking studies, e.g., Cant (1987, 1988), Dagosto (1995), Doran (1993), Fleagle (1976a), (Fleagle, 1976b), Fleagle and Mittermeier (1980), Garber and Pruetz (1995), Gebo and Chapman (1995a, 1995b), Mittermeier (1978), Mittermeier and Fleagle (1976), Morbeck (1977), and Susman *et al.* (1980). Additional historical details related to the study of primate positional behavior can be found in D'Aout and Vereecke (2011), Dagosto and Gebo (1998), and Garber (2011).

In another influential work, Napier and Napier (1967) presented a classification of primate locomotion which includes the following categories (with subcategories): Vertical Clinging and Leaping (including many lemurs, galagos, and tarsiers), Quadrupedalism (many Old and New World monkeys), Brachiation (gibbons and great apes) and Bipedalism (humans). This classification has been referenced and tested in a number of field studies of primate locomotion, including Cant (1987, 1988, 1992), Crompton (1986), Dagosto (1995), Doran (1992a, 1993), Fleagle (1976a, 1976b, 1977), Fleagle and Mittermeier (1980), Garber and Pruetz (1995), Hunt (1991), Mittermeier (1978), Mittermeier and Fleagle (1976), Morbeck (1977), Remis (1995), and Susman *et al.* (1980).

As noted by Dagosto and Gebo (1998), shortly after Ripley's seminal paper, a number of field studies on primate positional behavior were pursued and revealed that locomotor behavior is a complex activity intimately associated with morphology (e.g., Fleagle, 1976a, 1976b, 1977, 1978; Ward and Sussman, 1979), body size (e.g., Doran, 1993; Fleagle and Mittermeier, 1980;

Sugardjito and Vanhooff, 1986), ontogenetic development (e.g., Crompton, 1983; Rose, 1977), and a wide variety of ecological factors including support size (e.g., McGraw, 1998a, 1998b; Morbeck, 1977), diet (e.g., Garber, 1980, 1984), habitat structure (e.g., Garber, 1984; Morbeck, 1977; Rose, 1977), seasonality, and interspecific competition (e.g., Dagosto, 1995; Mittermeier, 1978). One of the most influential publications to come out during this time was Hunt *et al.* (1996) that provided standardized descriptions of primate locomotor and postural modes enabling researchers to collect data that are more generally comparable with one another. Throughout the first decade of the 21st century, researchers continued more intensive studies of primate positional behavior both in the field and laboratory, e.g., Aronsen (2004), Chatani (2003), Garber *et al.* (2005), Garber and Leigh (2001), Hirasaki *et al.* (2000), Isler and Gruter (2006), Lawler and Stamps (2002), McGraw (2000), Myatt *et al.* (2011), Myatt and Thorpe (2011), Off and Gebo (2005), Smith and Thompson (2011), Stafford *et al.* (2003), Thorpe and Crompton (2005, 2006), Wells and Turnquist (2001), Workman and Covert (2005), Workman and Schmitt (2012), and Wright (2005, 2007).

Laboratory studies (e.g., Hanna and Schmitt, 2011; Shapiro and Raichlen, 2005; Sockol *et al.*, 2007; Wallace and Demes, 2008; Young, 2009) shed light on the kinematic basis of the behaviors that were observed in living primates informing the relationship between morphological forms and positional modes in fossil primates. In fact, the positional modes of Hunt *et al.* (1996) are defined to reflect the kinematic basis of a given locomotor behavior. Application of lab biomechanical techniques in field studies has provided a more accurate understanding of the relationship between postural and locomotor modes and support use (such as quadrupedal gait selection) and is allowing more precise comparisons among different age classes and different individuals, among an array of environmental contexts (Blanchard and Crompton, 2011; Duarte *et al.*, 2012; Schmitt, 2011; Stevens *et al.*, 2011; Wunderlich *et al.*, 2011; Youlatos and Gasc, 2011).

The results from primate positional behavior studies have provided several important conclusions. First, sympatric primates are often characterized by significantly interspecific differences in patterns of positional behavior, body mass and musculoskeletal anatomy (Cannon and Leighton, 1994; Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995a, 1995b; McGraw, 1996a, 1998a, 1998b). Second, body mass is not as strong a predictor of positional behavior as originally assumed (see Dagosto, 1994; Dagosto and Yamashita, 1998; Gebo and Chapman, 1995b; McGraw, 1998a, 1998b, 2000; Youlatos, 1999, 2002). Third, interspecific differences in body mass and body size are characterized by particular behavioral and morphological adaptations that enable individual species to exploit resources in different ways (see Fleagle, 1999). Fourth, intraspecific differences in positional behavior vary little among adult males and adult females, especially during travel. However, within-species patterns of positional behavior during feeding are more variable and likely reflect seasonal changes in diet, day range, foraging strategies, activity pattern, and social interactions (see Chatani, 2003; Dagosto, 1995; Doran, 1993; Manduell *et al.*, 2011).

New methodologies are being employed in the field and laboratory to clarify relationships among positional behavior, habitat use, and anatomical structure (see D'Aout and Vereecke, 2011; Dagosto and Gebo, 1998). Although technologies such as digital videography and imaging, and more detailed behavioral ecological data are providing advances in positional behavior studies (Blanchard and Crompton, 2011; Duarte *et al.*, 2012; Guillot, 2011; Schmitt, 2011; Shapiro *et al.*, 2011; Stevens *et al.*, 2011; Wright *et al.*, 2008; Wunderlich *et al.*, 2011; Youlatos and Gasc, 2011) a number of important questions still remained to be answered with regard to the relationships among habitat, behavior, and morphology. For example the direct influences of body size, forelimb use, prehensile feet, and the arboreal substrate on gait choice are still open to question (e.g., Lemelin and Cartmill, 2010; Shapiro and Raichlen, 2005, 2006; Shapiro and Young, 2010; Vilensky and Larson, 1989). There has also been little research on the ontogeny of positional behavior in primates, which could help us to understand how selection may shape adult ecomorphological relationships by working upon different age classes (Bezanson, 2006a, 2006b, 2009; Biondi *et al.*, 2011; Wright, 2005; Young, 2005). Selection appears to act on age-related changes in body mass, limb and body proportions, and motor skills that effect an individual’s ability to exploit its environment (Bezanson, 2006a, 2006b, 2009; Biondi *et al.*, 2011; Lawler, 2006; Taylor, 1995; Wells and Turnquist, 2001; Workman and Covert, 2005; Wright, 2005). Thus, studies of primate positional behavior should be placed in context of primate life history strategies (Bezanson and Morbeck, 2013; Garber, 2011). Finally, greater attention on the energetic costs of locomotion and posture may deepen our understanding the patterns and modes of evolution among primates (Aronsen, 2004; Hanna and Schmitt, 2011; Liu *et al.*, 2009).

2.2.1. Variables that Influence Positional Behavior

One of the most frequently cited influences on primate positional behavior is body size. Based on biomechanical principles, body size is one critical factor influencing positional behavior and substrate preference of arboreal species, especially arboreal primates in the forest canopy (Cant, 1992; Fleagle and Mittermeier, 1980). One of Fleagle and Mittermeier’s (1980) most important conclusions was that for the seven sympatric platyrrhines in their study there were strong correlations between body size and locomotion. In a given arboreal habitat, larger-bodied animals leap less, climb more frequently, use more suspensory behavior, and bridge more often than smaller-bodied animals, or engage in relatively more frequent suspensory behavior. Some later studies have supported Fleagle and Mittermeier’s (1980) findings (e.g., Crompton, 1984; Youlatos, 1998b, 1999) while others have not (e.g., McGraw, 1998a). Comparing six cercopithecid species in the Tai Forest, Cote d’Ivore, McGraw (1998a) found no consistent association between body size and frequency of leaping during both travel and foraging with different trends for cercopithecines (i.e., smaller species leaped less) and colobines (i.e., smaller species leaped more), and an equivocal association between body size and climbing during both travel and foraging. Gebo and Chapman (1995b) found the opposite relationship observed by Fleagle and Mittermeier (1980) in their study of five cercopithecid species in Kibale Forest, Uganda. In Kibale, the smaller-bodied primates leaped less often and climbed more often than did the larger sympatric primates. Among New World primates, Garber (1991) found no clear association between body weight and leaping or climbing for three tamarin species.

Male and female primates often differ in their body size, the nutritional cost of reproduction, and social behaviors, and therefore significant sex-based differences in positional behavior might be expected (Garber, 2011). Doran (1993) studied adult common chimpanzee (*Pan troglodytes*) positional behavior and found males and females differ in arboreal locomotion while foraging, with males characterized by increasing climbing and females characterized by increased quadrupedal locomotion; but found "no significant sex differences in the frequency of overall (terrestrial + arboreal locomotion) chimpanzee locomotor activity" (p. 101). Remis (1995) found highly dimorphic male and female western lowland gorillas (*Gorilla gorilla gorilla*) to have similar patterns of positional behavior, and also have similar positional profiles during arboreal feeding postures. Sex-based differences documented for these gorillas included males squatting more frequently than females; and females exploiting smaller supports and spending more times in the periphery of tree crowns than males. However, these differences appeared to relate more to social interactions and social roles than to mechanical problems associated with body mass and weight support (Remis, 1995). Cant (1987), Thorpe (2009), and Thorpe and Crompton (2005, 2006) studied the positional behavior of male and female Sumatran orangutans (*Pongo pygmaeus*) and found that larger-bodied males tended to exploit larger supports than smaller-bodied females, and smaller-bodied females engaged in suspensory postures more frequently that did larger-bodied males. Males were found to sit and stand more during feeding. Gebo's (1992) study of two New World monkeys, and Gebo and Chapman's (1995b, 2000) study of five Old World monkeys found virtually no differences in positional behavior and substrate use (size and orientation) between males and females, even in highly dimorphic species. Grueter *et al.* (2013) found age- and sex-based differences in postures and substrate preference of *R. bieti* with the larger-bodied males of this highly dimorphic species frequenting the ground more than other age-sex classes. Adult males also used more solid substrates and less terminal branches than adult females and juveniles. Taken together, data on apes, Old World monkeys, and New World monkeys provide only limited evidence for significant sex-based differences in positional behavior and substrate use (e.g., Cant, 1987). This supports the contention that for many primate species patterns of positional behavior are highly conservative, at least among adult members (Garber, 2011).

At present, studies of ontogenetic effects on primate positional behavior are rare and have largely focused on older juveniles (e.g., Bezanson, 2006b; Biondi *et al.*, 2011; Covert *et al.*, 2004; Crompton, 1983; Doran, 1989; Sugardjito and Vanhooff, 1986; Turnquist and Wells, 1994; Wells and Turnquist, 2001; Workman and Covert, 2005; Wright, 2005) but offer critical insight into how factors such as body mass, motor skills, and development trajectories affect ecological and dietary distinctions between adult and immature individuals (Garber, 2011). Based on current evidence, it appears that in many primate species, including taxa that are characterized by a relatively short juvenile period and those characterized by a relatively long juvenile period, immature animals exhibit adult-like patterns of positional behavior at a relatively early age. For example, Bezanson (2006) found that young *Allouatta palliata* leapt significantly more often and bridged significantly less often than did adults, while *Cebus capucinus* only exhibited significant positional behavior differences at the most extreme age categories (adults vs. infants). Similarly, Wells and Turnquist (2001) found that young *Macaca mulatta* exhibited a more varied pattern of positional behavior, with greater contributions of different locomotor and postural categories, than did adults. Thorpe and Crompton (2005, 2006) also found no significant differences in the frequency of suspensory behaviors between adult and immature *Pongo abelii*. Taken together, data on apes, Old World monkeys, and New World monkeys provide only limited evidence for significant sex- and age-based differences in positional behavior and substrate use. This supports the contention that, for many primates, intraspecific patterns of positional behavior are highly conservative and constrained more by anatomy and neural development than body size (Garber, 2011).

Seasonal changes in the environment can affect diet, food availability and distribution, and activity patterns of primates living in tropical areas. This is expected to affect patterns of primate positional behavior as well. Studies of Dagosto (1995), Gebo and Chapman (1995a), Lemelin and Schmitt (2004), and McGraw (1998b) found that a higher degree of variability in positional repertoire during feeding may be associated with seasonal changes in diet, foraging strategies, and availability and distribution of feeding sites. Dagosto (1995, p. 811) concluded that "locomotion during travel appears to be fairly conservative while differences during feeding contribute substantially to the overall differences observed".

2.3. Odd-nosed monkeys

2.3.1. Taxonomy and Distribution

Four extant genera *Rhinopithecus*, *Pygathrix*, *Nasalis* and *Simias* are commonly referred to as the odd-nosed monkeys due to their unique external nasal morphology, which unites them in a clade distinct from other colobines (Brandon-Jones *et al.*, 2004; Groves, 2001; Jablonski, 1998; Jablonski *et al.*, 2011; Jablonski and Yan-Zhang, 1993; Kirkpatrick, 2011; Liedigk *et al.*, 2012; Peng *et al.*, 1993) (Table 2.1). The genus *Mesopithecus* which includes three extinct species: *M. pentelicus*, *M. monspessulanus*, and *M. delsoni* from late Miocene to late Pliocene deposits, and distributed in Eurasia from England to South China is sometimes grouped with the odd-nosed monkeys (Jablonski, 2002; Jablonski *et al.*, 2011; Radovic *et al.*, 2013). *Pygathrix* includes three species of doucs: *P. nemaeus*, *P. nigripes*, and *P. cinerea* distributed in Indochina (Vietnam, Laos, and Cambodia) (Nadler *et al.*, 2003; Nadler *et al.*, 2010). *Rhinopithecus* is comprised of five snub-nosed monkeys including three species (*R. roxellana*, *R. bieti*, and *R. brelichi*) endemic to southern China, *R. avunculus* endemic to northeastern Vietnam, and *R. strykeri* a newly discovered species from northern Myanmar and adjacent China (Geissmann *et al.*, 2011; Liedigk *et al.*, 2012; Long *et al.*, 2012). *Nasalis* contains a single species – the proboscis monkey (*N. larvatus*) inhabiting Borneo (Malaysia and Indonesia) (Bennett and Sebastian, 1988; Boonratana, 2000; Kirkpatrick, 2011; Yeager and Kirkpatrick, 1998). *Simias* also contains a single species – the simakobu (*S. concolor*) restricted to Mentawai Island (Indonesia) (Liedigk *et al.*, 2012; Tenaza, 1989; Tenaza and Fuentes, 1995). *S. concolor* was formerly placed in the genus *Nasalis* (e.g., Corbet and Hill, 1992; Groves, 1970). Jablonski (1998) and Groves (2001) treat *Simias* as a valid genus. A molecular analysis of Whittaker *et al.* (2006) supports this classification (Table 2.1).

Table 2.1. List of odd-nosed monkeys

Latin name	Common name	Distribution
Mesopithecus [1]		
Mesopithecus pentelicus		Late Miocene to Late Pliocene, southern and central Europe between 40° and 50° N and 0° to 30° E, Iran, and Afghanistan
M. monspessulanus		Pliocene, France and England through Romania and Greece
M. delsoni		Macedonia, Greece
Pygathrix		
Pygathrix nemaeus	Red-shanked douc	Vietnam, Lao, Cambodia
P. nigripes	Black-shanked douc	Vietnam, Cambodia
P. cinerea	Grey-shanked douc	Vietnam
Rhinopithecus		
Rhiopithecus roxellana	Golden snub-nosed monkey	China
R. bieti	Black snub-nosed monkey	China
R. brelichi	Gray snub-nosed monkey	China
R. avunculus	Tonkin snub-nosed monkey	Vietnam
R. strykeri [2]	Burmese snub-nosed monkey	Myanmar, China
Nasalis		
Nasalis larvatus	Proboscis monkey	Borneo island: Malaysia, Indonesia
Simias		
Simias concolor	Simakobu / Pig-tailed langur	Indonesia (Mentawai)

Note. [1] all *Mesopithecus* species are extinct, [2] this species was recently described by Geissmann *et al.* (2011)

2.3.2. Morphology

The odd-nosed monkeys are medium to large sized, sexually size dimorphic primates. The extinct *Mesopithecus* species are "medium size, with pronounced sexual dimorphism in the skull, dentition and postcranium" (Jablonski, 2002:260). All extant odd-nosed monkeys are relatively large and often exhibit pronounced dimorphism in body mass and canine size (Table 2.2).

2.3.3. Habitat and Density

While *Mesopithecus* fossils have been recovered in a wide area of Eurasia, the extant odd-nosed monkeys live in a variety of Asian forested environments ranging from northern temperate forests of the Tibet Plateau (*R. bieti*) to southern peat swamps of Borneo (*N. larvatus*). The population densities of odd-nosed monkeys vary among different populations of the same species as well as between species (Kirkpatrick, 2011). Density of each population and each species depends on its distribution range, locality, and human hunting pressures. *Pygathrix* species are distributed across Laos, Cambodia, and Vietnam to the east of the Mekong River, however, we lack good census data so estimates of population size and density for each of three doucs are limited. Recently, Lippold and Vu Ngoc Thanh (2008), and Streicher (2010) estimated 170-180 individuals of *P. nemaeus* in approximately 4,000 ha of core zone in Son Tra Nature Reserve, Da Nang City, Vietnam. Haus *et al.* (2009) provide estimates of 1,316 ± 871 *P. nemaeus* in an area of ca. 85,000 ha of Phong Nha-Ke Bang National Park, Vietnam. In Laos PDR, Coudrat *et al.* (2012) conducting a series of field surveys and literature review indicated this country contains the largest *P. nemaeus* population in the world. Ha Thang Long (2009) reported that 88 *P. cinerea* inhabit his study site of 1,000 ha in Kon Ka Kinh National Park, and about 200 grey-shanked doucs in this park's total area of 41,710 ha. Hoang Minh Duc (2007) recorded 470 *P. nigripes* in the strict protection area of 14,981 ha of Nui Chua National Park, and 163 individuals in the strict protection area of 16,041 ha of Phuoc Binh National Park, Vietnam. As with all species of odd-nosed monkeys, whether the populations are at carrying capacity for the environment is unknown.

The Chinese snub-nosed monkeys live in large bands of up to 400 individuals using a large home range of 2,600-3,500 ha (Bleisch and Xie, 1998; Kirkpatrick *et al.*, 1998; Ren *et al.*, 2008). However, the Tonkin snub-nosed monkey (*R. avunculus*) is restricted to small and isolated habitats. In Khau Ca area of Ha Giang Province, Vietnam, home to the largest population of this species there appears to be approximately 100 individuals living in a 700-ha primary forest. In other sites such as Na Hang Nature Reserve and the Tung Vai forest, estimates of population densities are not available due to a lack of reliable population estimates (Covert *et al.*, 2008; Le Khac Quyet and Covert, 2010; Le Xuan Canh *et al.*, 2008; Thach Mai Hoang, 2011). *N. larvatus* has high density varying from 10 to 63 individuals/km^2 and its home range varies from 130 to 770 ha (Bennett and Sebastian, 1988; Yeager, 1989, 1990, 1991, 1992; Yeager and Kirkpatrick, 1998). As noted above, *S. concolor* is restricted to Mentawai Island and its home range is estimated to be 3.5-20 ha with population densities of 8-220 individuals/km^2 (Tenaza and Fuentes, 1995; Watanabe, 1981).

2.3.4. Feeding Ecology

The odd-nosed monkeys inhabit a wide range of environments and vary in feeding behavior. Anatomical adaptations for ingesting and digesting leaves including “sharp molars to chew leaves, enlarged salivary glands that help degrade them, and a multi-chambered stomach with symbiotic microbes that break down leaf fibers” (Kay and Davies, 1994). The diets of odd-nosed monkeys include leaves, fruits, seeds, flowers, and other plant parts.

Table 2.2. Morphological features of extant odd-nosed monkeys

Latin name	Body mass (kg)	Head-Boby Length (HBL) (cm)	Tail Length (%HBL)	Dorsum	Venter	Crest on crown	Cheeks	Hand and feet
Pygathrix								
Pygathrix nemaeus	6.6 – 8.3 (♀) 8.6 – 11.0 (♂)	55-82	C. 110	Grey	White			White
P. nigripes	C. 8.0 (♀) C. 11 (♂)	50-56	C. 110	Dark grey	White			Black
P. cinerea	7.5 – 9.4 (♀) 10.7 – 12.4 (♂)	56-64	C. 110	Light grey	Light grey			Light grey
Rhinopithecus								
Rhiopithecus bieti	9.2 (♀) 15.0 (♂)	74-83	70-90	Dark grey	White	Long	White	Black
R. roxellana	6.5 – 10.0 (♀) 15.0 – 39.0 (♂)	66-76	85-95	Dark grey-brown	Pale orange	Short	Orange	Yellowish
R. brelichi	7.8 (♀) 13.3 – 15.8 (♂)	–	–	–	Yellowish brown	–	–	Blackish
R. avunculus	7.0 – 9.0 (♀) 13.0 – 22.0 (♂)	51-61	140-150	Blackish	Orange	None	Yellow	Black
R. strykeri	–	55.5	140	Black	Black	–	–	Black
Nasalis								
Nasalis larvatus	12.0 (♀) 24.0 (♂)	–	C. 110-120	Yellowish	–	None	Yellowish	Light grey
Simias								
Simias concolor	C. 7.0	–	C. 30	Blackish	Blackish	Blackish	Blackish	Blackish

Sources: Corbet and Hill (1992), Groves (1970), and Kirkpatrick (2011)

Both Hoang Minh Duc (2007) and Rawson (2009) have conducted long-term studies of feeding by *P. nigripes* documenting diets of leaves (young and mature) (39.96-54.6%), fruits (11.38-29.34%), flower (8.78-14.56%), seeds (0-39.70%) and others (0.18-1.5%). *R. avunculus* at Khau Ca area consumes plant parts including leaf stems (27.78%), young leaves (flush leaves) (11.11%), unripe fruits (22.22%), inflorescences and flowers (8.33%) and seeds (2.78%) (Le Khac Quyet *et al.*, 2007). The Chinese *Rhinopithecus* species live in temperate forests with snow cover during the winter months. To survive in such a harsh environment, their diet in winter consists primarily of lichen, and green bark and buds of dicot plants; in other seasons, they eat leaves, fruits, seeds, flowers and other plant parts (Bleisch and Xie, 1998; Kirkpatrick and Grueter, 2010; Kirkpatrick *et al.*, 1999; Kirkpatrick *et al.*, 2001). *N. larvatus* consumes a diet of leaves (41-74%), fruits and seeds (11-58%) and other plant parts (5-8%) (Bennett and Sebastian, 1988; Yeager, 1989). Paciulli (2013) reported *S. concolor* consumes a diet of young leaves (30%), fruits (30%), seeds (15%), unspecified leaves (15%), mature leaves (5%), and buds, insect larvae and insects (6%).

2.3.5. Social Behavior and Organization

Social and sexual behavior of odd-nosed monkeys is poorly known in part due to a lack of long term research. There appears to be some interesting variation in social organization cross the odd-nosed monkeys (Kirkpatrick and Grueter, 2010). Most authors agree that at the core of the odd-nosed monkeys' social organization is the one male unit (OMU) and also note the presence of bachelor male units (AMU). OMUs and AMUs often travel and feed together as a band. Group size of OMU varies between different populations of the same species as well as different species (Bleisch and Xie, 1998; Boonratana and Le Xuan Canh, 1998; Hoang Minh Duc, 2007; Kirkpatrick, 2011; Kirkpatrick *et al.*, 1998; Su *et al.*, 1998). Kirkpatrick (2011) argued that Asian colobine sex is initiated by females. Ren *et al.* (1995) report that female *R. roxellana* uses the "crouch" to signal sexual proceptivity and encourage male mounting. I have also observed this in *R. avunculus*. *S. concolor* is the only Asian colobine having sexual swellings to indicate receptivity (Tenaza, 1989). *R. roxellana* has a gestation of 6-7 months (Qi *et al.*, 2008; Qi *et al.*, 2011). Studies of *R. bieti* and some other Asian colobines report that their interbirth intervals are around two years and vary between different populations of the same species (Kirkpatrick, 2011; Kirkpatrick and Grueter, 2010).

2.3.6. Locomotion

Most of the odd-nosed monkeys are habitually arboreal. *R. roxellana* is both arboreal and terrestrial, spending almost half of its time on the ground (Su *et al.*, 1998). *R. bieti* is also semi-terrestrial, spending between 20 and 80% of the day on the ground (Grueter *et al.*, 2013; Isler and Gruter, 2006). *R. brelichi* is primarily arboreal, and its locomotion is characterized by quadrupedal walking, climbing, leaping, semi-brachiation and occasionally by full brachiation (Bleisch *et al.*, 1993; Bleisch and Xie, 1998). *R. avunculus* is habitually arboreal in that they only rarely come to the ground in Khau Ca and forelimb suspension is commonly used in both locomotion and postures (Covert *et al.*, 2008). *Pygathrix* species are predominantly arboreal and also reported to use forelimb suspensory postures and locomotion (Byron and Covert, 2004; Rawson, 2009; Workman and Covert, 2005; Wright *et al.*, 2008). The locomotion of *N. larvatus* includes semi-brachiation, climbing, leaping, quadrupedal and suspensory movement and rare bipedalism. They are also good swimmers and they can swim underwater for up to 20 m (Bennett and Sebastian, 1988; Gron, 2009). Locomotion of *S. concolor* is characterized by quadrupedal locomotion, leaping, climbing, and brachiation (Paciulli, 2013). Odd-nosed monkeys use vertical climbing and suspensory behaviors that are similar to those exhibited by atelines and hominoids (Byron and Covert, 2004; Isler and Grueter, 2006), but not usually found in other Old World monkeys. In terms of positional behavior, Su and Jablonski (2011) reported the odd-nosed monkeys exhibit unique locomotor behaviors that are not usually found in other Old World monkeys, such as arm-swinging, brachiation and vertical climbing. They resemble apes and atelines in some morphological traits that are not seen in other colobines. Su and Jablonski (2011, p. 190) noted that “the odd-nosed monkeys present a natural experiment in comparative morphology". They also stated that odd-nosed monkeys more closely resemble apes and atelines than other colobines in some forelimb traits and indices like relative olecranon length, and scapular and intermembral indices that are regarded as association with vertical climbing and suspensory behaviors (Fleagle, 1976a, 1976b).

2.3.7. Conservation Status

All extant odd-nosed monkeys are listed as endangered or critically endangered (IUCN, 2013). Of particular interest is the inclusion of *P. cinerea*, *R. avunculus*, and *S. concolor* in the world's top 25 most endangered primates list (Mittermeier *et al.*, 2012) as well as Critically Endangered (IUCN, 2013; Le Xuan Canh *et al.*, 2008). In addition, *R. strykeri* is listed as critically endangered whereas the other odd-nosed species are listed as endangered (EN) in the IUCN Red List of Threatened Species (IUCN, 2013). The primary threats to odd-nosed monkeys are hunting, loss of habitat, and habitat disturbance (IUCN, 2013; Mittermeier *et al.*, 2012; Nadler *et al.*, 2003).

2.4. Tonkin Snub-nosed Monkey (*Rhinopithecus avunculus*)

2.4.1. Morphology

The Tonkin snub-nosed monkey was first described by Dollman (1912) as *Rhinopithecus avunculus* based on two specimens collected in September 1911 by Alan Owston and Hyojiro Orii in Yen Bai Province. The upper parts of the body of *R. avunculus* are dark brown, its forehead and cheeks are creamy, the face is bluish white with large pink lips, and the side of the neck is orange buff. The belly and the inner side of the limbs are creamy white. On the outside of the arms and legs a stripe of the same color as the back runs to thighs and feet and there is a white patch on the elbows inside the black stripe. There is a buffy white patch on the rump on either side of the tail, where there is a small orange collar. The tail is very long, with brown to black hairs and a white tassel. The ears are tufted; the hands and feet are black. The nose is upturned and has tips (Groves, 1970; Nadler *et al.*, 2003; Napier and Napier, 1967) (Figure 2.1). Table 2.3 provides physical measurements of *R. avunculus*. Unfortunately we do not have a skeletal sample for *R. avunculus* so direct comparisons cannot be made with the other members of this genus or the closely related genera. Outward appearance, however, suggests that there might be greater similarity to some of the doucs in body proportions and other aspects of morphology. This shared pattern of anatomy across taxa could be interpreted to suggest that *R. avunculus* more closely resembles the common ancestor of *Rhinopithecus*.

Table 2.3. Physical measurements of *R. avunculus*

Index	♂ (n = 3)	♀ (n = 7)	Mean (n = 10)
Head and body (mm)	658.33	520.00	561.50
	(640 – 670)	(484 – 565)	(484 – 670)
Tail (mm)	823.00	685.71	726.90
	(820 – 850)	(660 – 725)	(660 – 850)
Hind foot (mm)	217.67	173.29	186.60
	(210 – 223)	(150 – 190)	(150 – 223
Ear (mm)	44.00	28.00	32.80
	(43 – 45)	(12 – 40)	(12 – 45)
Body mass (kg)	14.9	7.9	10.2
	(13.0 – 16.0)	(7.0 – 9.0)	(7.0 – 16.0)

Source: Pham Nhat (1993)

Figure 2.1. A group of Tonkin snub-nosed monkeys (*R. avunculus*)

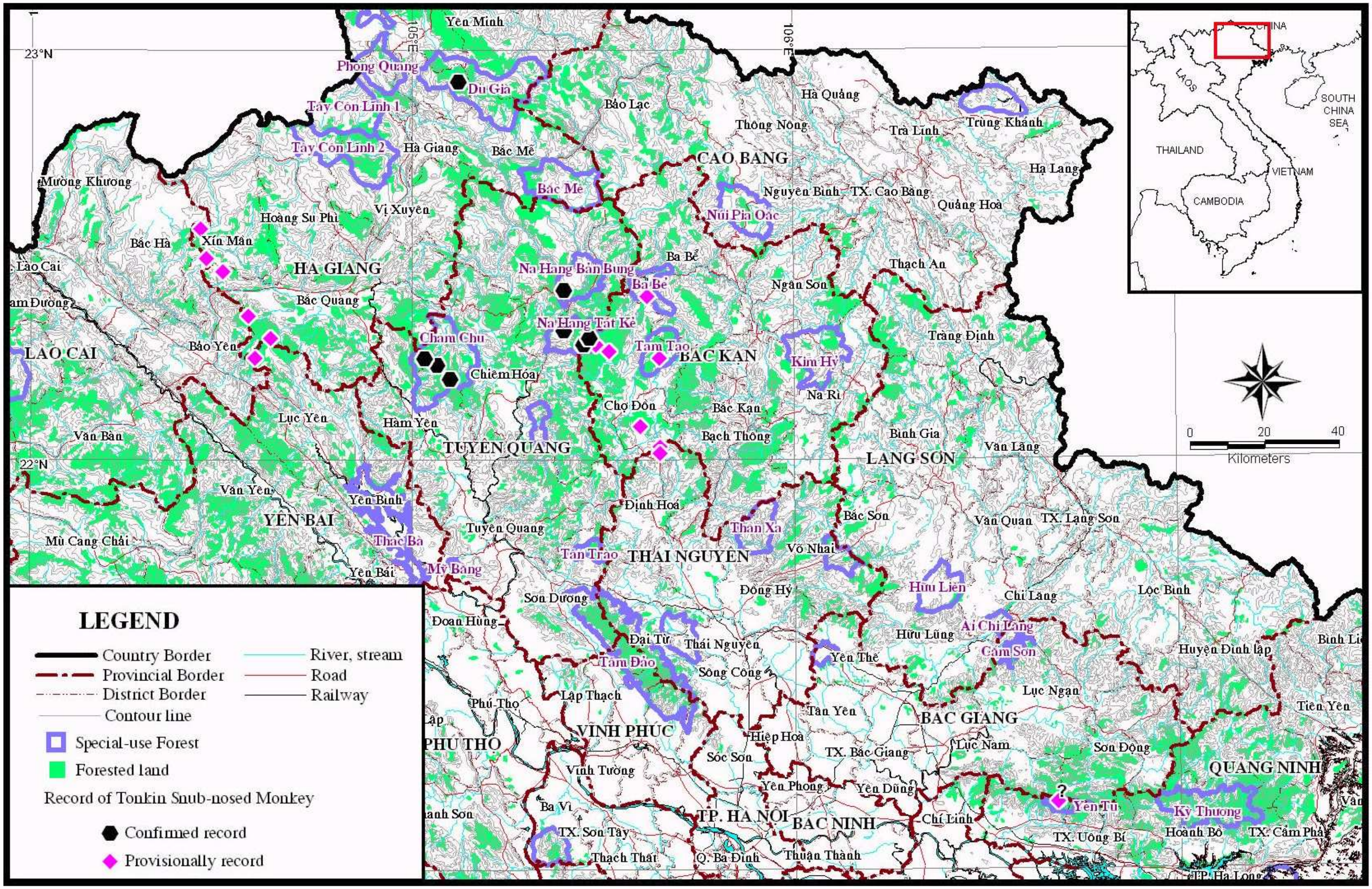

Figure 2.2. Distribution map of *R. avunculus*

2.4.2. Distribution

The Tonkin snub-nosed monkey is found only in northern Vietnam. The geographic distribution of this species is 21°37'- 22° 25'N and about 104°47' - 106°53'E (Fooden, 1996). During surveys in the winter of 1926 -1927, Delacour and Lowe collected 12 *R. avunculus* specimens in Bac Kan Province (Thomas, 1928). Groves (1970) reported the presence of this species near Bach Thong and Yen Bai (Lao Cai Province). Specimens deposited in the Hanoi Zoological Museum came from Luc Yen District (Yen Bai Province), Na Hang District (Tuyen Quang Province), and districts of Bach Thong, Cho Don, Ban Thi and Dinh Hoa (Bac Kan Province).

R. avunculus lives in semi- and evergreen forests at 200 – 1,200 m above mean sea level (a.m.s.l.). Other snub-nosed monkeys live in the high montane temperate forests at altitude of much higher than 1,200 m a.m.s.l. (Boonratana and Le Xuan Canh, 1998; Covert *et al.*, 2008; Le Khac Quyet and Covert, 2010; Ren *et al.*, 1998).

2.4.3. Feeding Ecology

The Tonkin snub-nosed monkey primarily consumes plant parts including leaves, fruits and seeds. Pham Nhat (1994) reported that *R. avunculus* ate leaves as their major food and also included bamboo in their diet. However, more recent studies have demonstrated that the diet of *R. avunculus* includes a substantial amount of fruits (Boonratana and Le Xuan Canh, 1998; Covert *et al.*, 2008; Dong Thanh Hai, 2007, 2011; Le Khac Quyet *et al.*, 2007). In Na Hang, Boonratana and Le Xuan Canh (1998) observed 34 feeding bouts, and the diet consisted of young leaves (38%), unripe fruits (47%), and ripe fruits and seeds (15%). In Khau Ca area, *R. avunculus* consumes food items of at least 34 plants species; leaf stems and fruits are the most common part of the their diet (27.78%), followed by young leaves (flush leaves) (11.11%), unripe fruits (22.22%), inflorescences and flowers (8.33%) and seeds (2.78%). The plant foods most frequently consumed by *R. avunculus* are *Iodes seguini* (leaf stems and ripe fruits), *Garcinia* spp. (leaf stems), *Acer tonkinense* (leaf stems), *Excentrodendron tonkinensis* (fruits and flowers), and *Brassaiopsis stellate* (ripe fruits). The toughness of the diet of *R. avunculus* was also found to exceed that of other Southeast Asian colobines (Covert *et al.*, 2008; Le Khac Quyet *et al.*, 2007).

2.4.4. Social Behavior and Organization

Social and sexual behavior of *R. avunculus* is poorly known due to the lack of long term research on their socioecology. Boonratana and Le Xuan Canh (1998), and Dong Thanh Hai (2007, 2011) noted that *R. avunculus*' social organization is similar to that of other odd-nosed monkeys with one-male units (OMUs) being the core and also all-male units (AMUs) are present. The OMUs and AMUs often travel and feed together. There has been no record of fighting between adult males. Similar to other odd-nosed monkeys, *R. avunculus* sex is initiated by females using a "crouch" to signal sexual perceptivity and encourage male mounting (Dong Thanh Hai *et al.*, 2011).

2.4.5. Locomotion

R. avunculus is habitually arboreal and only rarely travel on the ground (Dong Thanh Hai, 2011). Covert *et al.* (2008) reported a list of locomotor and postural modes used by *R. avunculus* including: a symmetrical gait walk, quadrupedal running, vertical climbing, rump-first descent, brachiation, brachiating leap, arrested drops, pronograde leaping, pumping leaping, and quadrupedal drop, and sit out, sit/forelimb suspend, chair sit, bimanual cling, cling/forelimb suspend, stand/forelimb-suspend, forelimb-suspend/stand, and lie. In particular, forelimb suspension is commonly used in locomotion and postures.

2.4.6. Conservation Status

R. avunculus is endemic to a small area in northern Vietnam, and only approximately 200-250 *R. avunculus* exist today in Tuyen Quang and Ha Giang Provinces (Le Khac Quyet and Covert, 2010). Moreover, it is listed as Critically Endangered in the IUCN Red List of Threatened Species (IUCN, 2013; Le Xuan Canh *et al.*, 2008) and as Critically Endangered in the Red Data Book of Vietnam (Ministry of Science & Technology and Vietnam Academy of

Science & Technology, 2007). Recently, *R. avunculus* was also listed in the World's top 100 threatened species (Baillie and Butcher, 2012). Threats to *R. avunculus* throughout its range include hunting for traditional medicine and habitat loss and degradation (Covert *et al.*, 2008; Nadler *et al.*, 2003; Nadler *et al.*, 2010). Also, as reviewed by Le Xuan Canh and Boonratana (2006) and Le Khac Quyet and Covert (2010) this species is only known from four areas today and the populations at two of these areas, Cham Chu and Na Hang, have experienced rapid declines during the past decade (Table 2.4).

Table 2.4. Number and distribution of *R. avunculus* in Vietnam

Location	**Population number**	**Sources**
Khau Ca area, Ha Giang	> 100	Field observations in this study
Tung Vai area, Ha Giang	20 – 40	Le Khac Quyet and Covert (2010)
Na Hang Nature Reserve, Tuyen Quang	15 – 20	Thach Mai Hoang (2011)
Cham Chu Nature Reserve, Tuyen Quang	0 – 20	Dong Thanh Hai *et al.* (2006)

Because of the lack of field reports published in international sources following the initial reports by Dollman (1912) and Thomas (1928) Mittermeier and Cheney (1987:488) stated that the "Vietnamese snub-nosed monkey (*Rhinopithecus avunculus*) from Tonkin may already be extinct. It is known from only a handful of museum specimens collected earlier in this century, and there are no recent reports of it from the wild." In the book Primate Conservation Biology, Cowlishaw and Dunbar (2000) also use *R. avunculus* to symbolize a primate on the brink of extinction. Since 2002, *R. avunculus* has been included in the biennial list of the world top's 25 endangered primates (Mittermeier *et al.*, 2012). According to the *Conservation Action Plan for the Tonkin snub-nosed monkey in Vietnam* (Le Xuan Canh and Boonratana, 2006), the highest priorities for protecting this species are: 1) to arrest any further decline in populations and habitats, and 2) to secure protection of their habitats available through establishing new protected areas, extensions of existing ones, or establishing land corridors between protected areas within 3- to 5-year goals. To date these goals have not been met beyond some of our ongoing work at

Khau Ca. Conservation efforts for *R. avunculus* would benefit greatly by behavior ecological studies and conservation activities with involvement of national and international institutions, conservationists and conservation practitioners.

2.5. Primate Conservation in Vietnam

According to the primate taxonomy of Groves (2001) and the Asian primate classification of Brandon-Jones *et al.* (2004) as well as updated data of primate taxonomy and the description of a new gibbon in 2010, Vietnam's primate fauna comprises 25 taxa belonging to three families: Loridae (lorises), Cercopithecidae (macaques and colobines) and Hylobatidae (gibbons) (Table 2.5).

Vietnam's primates are one of the top global priorities for primate conservation. There are seven primate taxa are Critically Endangered (CR), eight are Endangered (EN) and four are Vulnerable (VU) as listed in the IUCN Red List of Threatened Species (IUCN, 2013), and five of them have been consistently included on the list of the world's top 25 most endangered primates (Mittermeier *et al.*, 2012). There are four endemic species and subspecies including the Tonkin snub-nosed monkey (*R. avunculus*), Delacour's langur (*Trachypithecus delacouri*), Cat Ba langur (*T. poliocephalus poliocephalus*), and grey-shanked douc (*Pygathrix cinerea*).

Vietnam's primates are threatened by illegal hunting and trading, and habitat loss and fragmentation. They are hunted for bush meat and traditional medicine. Many Vietnamese still believe that the meat of primates is rich in nutrients and the balms made from their bones are a healthy and beneficial medicine (Nguyen Manh Ha *et al.*, 2008). As a developing country having a territory just larger than the state of Colorado, and with a population of about 90 million, the Vietnamese people place great demands on land and natural resources. Demand of land for agricultural and development purposes are the main causes of habitat loss. Between 1990 and 2010, Viet Nam lost an average of 221,700 ha of forest or 2.37% per year (FAO, 2010). This is clear documentation of dramatic habitat loss in Vietnam. Timber extraction (both legal and illegal) causes habitat fragmentation and degradation. At present, Vietnam's forest coverage is about 40% of total land but primary forests are only about 17% of forest coverage (FAO, 2010). Illegal wildlife trade at both the local and international levels, including primates, is serious problems for conservation in Vietnam (Nadler *et al.*, 2010).

Table 2.5. List of primates in Vietnam

Common name	Latin name	Conservation status		
Loridae		Vietnam	IUCN	Top 25
Slow loris	*Nycticebus bengalensis*	V	VU	
Pygmy loris	*N. pygmaeus*	V	VU	
Cercopithecidae				
Cercopithecinae				
Stump-tailed macaque	*Macaca arctoides*	V	VU	
Assam macaque	*M. assamensis*	V	NT	
Long-tailed macaque	*M. fascicularis*	V	LC	
Pig-tailed macaque	*M. leonina*	V	VU	
Rhesus macaque	*M. mulatta*	V	LC	
Colobinae				
Red-shanked douc	*Pygathrix nemaeus*	E	EN	
Black-shanked douc	*P. cinerea*	E	CR	X
Grey-shanked douc	*P. nigripes*	E	EN	
Tonkin snub-nosed monkey	*Rhinopithecus avunculus*	E	CR	X
Grey langur	*Trachypithecus phayrei*	V	EN	
Delacour’s langur	*T. delacouri*	E	CR	X
Francois’ langur	*T. francoisi*	E	EN	
Ha Tinh langur	*T. hatinhensis*	E	EN	
Cat Ba langur	*T. p. poliocephalus*	E	CR	X
Indochinese silvered langur	*T. germaini*	V	EN	
Annamese silvered langur	*T. margarita*	V		
Hylobatidae				
Black-crested gibbon	*Nomascus concolor*	E	CR	
Cao vit gibbon	*N. nasutus*	E	CR	X
Northern white-cheeked gibbon	*N. leucogenys*	E	CR	
Southern white-cheeked gibbon	*N. siki*	E	EN	
Yelow-cheeked gibbon	*N. gabriellae*	E	EN	
Northern buffed-cheeked gibbon	*N. anamensis*			

Sources: IUCN (2013), Mittermeier *et al.* (2012)

Note. E – Endangered, V – Vulnerable
CR – Critically Endangered, EN – Endangered, VU – Vulnerable, LC – Least Concerned
X – in the list

Vietnam has taken active measures to protect biodiversity including primates during the past few decades. The standard conservation approaches and tools commonly used for biodiversity have been applied to Vietnam's remaining primate populations. In 1992, Vietnam issued the first Red Data Book listing all of Vietnam's primates. This book has been recently revised in 2007 (Ministry of Science & Technology and Vietnam Academy of Science & Technology, 2007). In addition, in 1992, The Vietnam Government also issued the first decree regulating the list of rare and precious flora and fauna and their management and protection (Decree No. 18/HDBT). This decree and its appendices provided legislation for management and protection of wildlife including primates. In response to changing conservation issues this has been replaced by newer decrees issued in 2002 and 2006. The Biodiversity Law was adopted in 2008 and has a strong focus on biodiversity conservation in Vietnam. Notably, primates have been listed as target species in Vietnam's Biodiversity Action Plan (1995). In 2006, the Tonkin Snub-nosed Monkey Conservation Action Plan was published and included a detailed list of conservation activities needed to protect this critically endangered and endemic monkey (Le Xuan Canh and Boonratana, 2006).

During the past decades, there has been a system of 30 national parks and 134 nature reserves established throughout Vietnam to conserve biodiversity including threatened primates. Remarkably, some of these protected areas have prioritized primates as flagship species for their conservation such as the Delacour's langur (*T. delacouri*) in Cuc Phuong National Park and Van Long Nature Reserve, Hatinh langur (*T. hatinhensis*) in Phong Nha – Ke Bang National Park, Cao Vit gibbon (*N. nasutus*) in Cao Vit Gibbon Species/Habitat Conservation Area, western black-crested gibbon (*N. concolor*) in Mu Cang Chai Species/Habitat Conservation Area, and the Tonkin snub-nosed monkey in Na Hang Nature Reserve (Tuyen Quang Province) and Tonkin Snub-nosed Monkey Species/Habitat Conservation Area at Khau Ca (Ha Giang Province).

Primate conservation has received significant attention in Vietnam where there have been various primate conservation projects implemented in the past two decades. These projects have helped to save Vietnam's endangered primates. Noteworthy successful projects include the

‘Endangered Primate Rescue Center’ project in Cuc Phuong National Park (1993 to present), Tonkin Snub-nosed Monkey Conservation Projects in Khau Ca (2004 to present), Cat Ba Langur Conservation Project in Cat Ba National Park (2000 to present), and Cao Vit Gibbon Conservation Project in Cao Bang Province (2002 to present).

In recent years, behavioral and ecological studies of primates have increased in Vietnam including projects by both Vietnamese scientists: Drs. Hoang Minh Duc, Ha Thang Long, and Dong Thanh Hai, and foreign scientists: Drs. Catherine Workman, Larry Ulibarri, Marina Kenyon, and Jonathan O’Brien. There have also been more and more publications about Vietnam’s primates published in national and international journals and conferences, e.g., Blair *et al.* (2011), Boonratana and Le Xuan Canh (1998), Byron and Covert (2004), Dong Thanh Hai (2011), Fan *et al.* (2012), Ha Thang Long (2009), Haus *et al.* (2009), Hoang Minh Duc (2007), Hoang Minh Duc *et al.* (2009), Le Khac Quyet and Covert (2010), Le Khac Quyet *et al.* (2007), Lippold and Vu Ngoc Thanh (2008), Nadler *et al.* (2003), Nguyen (2000), Sterling and Hurley (2005), Van Ngoc Thinh *et al.* (2010), Workman (2010), Workman and Covert (2005), Workman and Schmitt (2012), and Wright *et al.* (2008). Some of this work can be characterized as important symbolic achievements for primate studies and conservation in Vietnam and examples include the rediscovery of the Tonkin snub-nosed monkey in 1990, establishment of the first Endangered Primate Rescue Center (EPRC) in 1993, the discovery and successful conservation of a new Tonkin snub-nosed monkey population in Ha Giang Province and descriptions of new species, the Grey-shanked douc (*Pygathrix cinerea*) in 1997 (Nadler, 1997) and the Northern buff-cheeked gibbon (*Nomascus annamensis*) in 2010 (Van Ngoc Thinh *et al.*, 2010).

CHAPTER III

STUDY SITE, SUBJECTS, AND METHODS

3.1. Introduction

In this chapter, I present information on the study site, subjects, and general methods that were used for data collection and analysis throughout this study. Individual chapters contain more detailed information such as the statistical tests and methods that are most relevant to the part of the analysis covered.

3.2. Tonkin Snub-nosed Monkey Species/Habitat Conservation Area at Khau Ca

3.2.1. General Information

The Tonkin snub-nosed monkey (*R. avunculus*) was first described by Guy Dollman (1912) based on two specimens collected in September 1911 by Alan Owston and Hyojiro Orii in Yen Bai Province. Following a number of decades without field reports on its status, (Mittermeier and Cheney, 1987) (1986:488) stated that the “Vietnamese snub-nosed monkey (*Rhinopithecus avunculus*) from Tonkin may already be extinct. It is known from only a handful of museum specimens collected earlier in this century, and there are no recent reports of it from the wild”. While not extinct, it is extremely rare. In 1989, a population of *R. avunculus* was confirmed in Na Hang – Chiem Hoa region of Tuyen Quang Province (Ratajszczak *et al.*, 1992) that led to the establishment of the Na Hang Nature Reserve and number of conservation activities in this nature reserve (Boonratana, 1999; Boonratana and Le Xuan Canh, 1998; Martin, 2004). In 2001, another population of *R. avunculus* in Tuyen Quang Province was confirmed on Cham Chu Mountain and then the Cham Chu Nature Reserve was established in the same year.

However, conservation efforts at Na Hang and Cham Chu largely failed for various reasons and *R. avunculus* populations have declined rapidly during the past decade (Dong Thanh Hai, 2007, 2011; Dong Thanh Hai *et al.*, 2006; Le Khac Quyet and Covert, 2010; Thach Mai Hoang, 2011).

Ha Giang Province was not originally included in the reported historical distribution of *R. avunculus* (Boonratana and Le Xuan Canh, 1998; Fooden, 1996; Ratajszczak *et al.*, 1992). In January 2002, a population of 50-60 *R. avunculus* was discovered in Khau Ca area (Le Khac Quyet, 2002, 2004). As conservation activities immediately initiated in the Khau Ca area, in contrast to Na Hang and Cham Chu Nature Reserves, the Khau Ca area has seen a number of successes. Since 2003, conservation activities including population and habitat monitoring, conservation education and raising awareness, law enforcement, and behavioral ecological studies have been conducted. As a result, the Khau Ca population is growing and relatively well-protected. At present, the best estimation is that there are more than 100 *R. avunculus* in the Khau Ca Forest (Dong Thanh Hai, 2007, 2011; *field observations in this study*). In fact, Khau Ca is now recognized as being home to the only viable population of this species thus Covert *et al.* (2008) noted that Khau Ca is critically important location for conservation of *R. avunculus*.

The Tonkin Snub-nosed Monkey Species/Habitat Conservation Area at Khau Ca (hereafter referred as TSNM SHCA at Khau Ca) was established by the Decision No. 3115/QD-UBND of Ha Giang Provincial People’s Committee dated on August 26, 2009, and its management board established by Decision No. 56/QD-KL of Ha Giang Forest Protection Department. According to the Decision No. 3115/QD-UBND, the TSNM SHCA at Khau Ca is located between 22^{o}49’ – 22^{o}52’ N and 105^{o}05’ – 105^{o}09’ E, and is about 20km to the east of Ha Giang City (Figure 3.1). Its total area is 2,024.2ha and it is located in three communes: Tung Ba (Vi Xuyen District), Minh Son and Yen Dinh (Bac Me District). This protected area was established with the primary goal of providing long term protection of the *R. avunculus* population and its habitat as well as other biodiversity in the Khau Ca area.

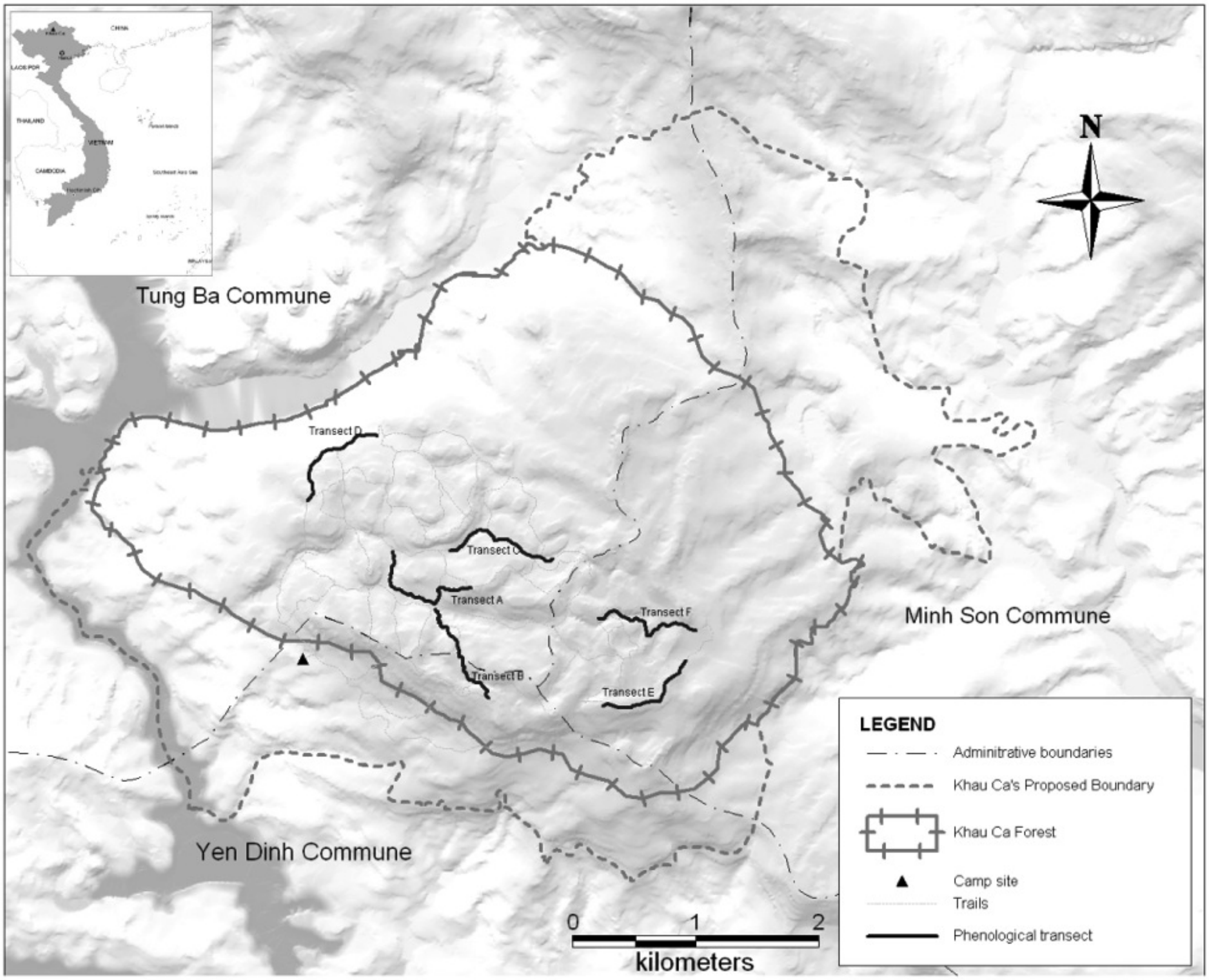

Figure 3.1. Map of Khau Ca Forest, Ha Giang Province, northeastern Vietnam

The TSNM SHCA at Khau Ca is a typical limestone area. Its terrain is characterized by deep, narrow valleys, with sharp, loose outcrops. The elevation ranges from 400 meters above sea level (m.a.s.l.) (Tung Ba Commune center) to 1341 m.a.s.l. (Coc Moc Peak). The average slope is 30°. At 600-700 m, it is apparent that the forest has undergone high levels of agricultural disturbance in the recent past, and is presently composed of scrub and small trees while at 700-1,400 m the forest is markedly less disturbed, supporting various old, tall trees in the valleys and short trees distributed on mountain tops and ridges (Nguyen Anh Duc *et al.*, 2006b).

The core zone of TSNM SHCA at Khau Ca is Khau Ca Forest lies on a block of limestone within a landscape of villages and agricultural land, punctuated by forested limestone outcrops and mountains. There are no water sources in Khau Ca Forest because of its porous limestone terrain associated with the steep elevations and porosity. The forest is located in the watershed of the Gam River, which joins the Lo River near Tuyen Quang town, and then they join the Red River at Viet Tri City, Thai Nguyen Province.

The nature reserve is surrounded by ten local villages having 614 households of 3,441 people. The largest ethnic group is Tay with 2,542 people (73.9%), followed by 768 Dao (22.3%), 103 Hmong (3.0%), and 28 others (0.8%) (Nguyen Hung Manh and Pham Hoang Linh, 2006). Local communities extract forest resources, including those of the Khau Ca Forest, for a variety of uses including timber for housing, firewood, medicinal plants, and other non-timber forest products (Nguyen Hung Manh and Pham Hoang Linh, 2006; Tran Chi Trung *et al.*, 2002; Tran Phung and Truong Thanh Nam, 2008; Tran Van On and Nguyen Quoc Huy, 2004).

3.2.2. Climate

Khau Ca Forest is located within the sub-tropical region of northern Vietnam and is characterized by a tropical monsoon climate.

Monthly temperatures were collected from January 2009 to December 2010 at the Ha Giang Meteorological Station and ranged between 6.0 °C (January 2009) to 37.3 °C (August 2009). June to August were the hottest months (monthly mean temperatures of 27.8 – 28.6 °C) and December to January the coolest (monthly mean temperatures of 14.2 – 18.0 °C). Average temperature for the year 2009 and 2010 was 23.4 °C and 23.9 °C respectively (Figure 3.2).

Total rainfall was 2,343.7 mm in 2009 and 2,550.1 mm in 2010. The dry season (< 100 mm rainfall/month) extends from October to March and the rainy season from April to September (≥ 100 mm rain/month) (Figure 3.3.).

3.2.3. Vegetation and Plant Richness

The forest in Khau Ca may generally be described as lower montane evergreen limestone forest and dominated trees include *Excentrodendron tonkinense* (Tiliaceae), *Garcinia* spp. (Clusiaceae), *Pometia pinnata* (Sapindaceae), *Diospyros* spp. (Ebenaceae), *Vernicia* spp. (Euphorbiaceae), *Acer* spp. (Aceraceae), *Schefflera* spp. (Araliaceae), and *Quecus* sp. (Fagaceae) (Nguyen Anh Duc *et al.*, 2006b).

Following Thai Van Trung's forest vegetation classification system (1978, 2000), Nguyen Anh Duc *et al.* (2006b) and Vu Anh Tai *et al.* (2009) determined five vegetation types in Khau Ca Forest as follows:

- Primary evergreen lower montane forest predominates on the limestone. It consists primarily of broad-leaf evergreen trees of Tiliaceae (*Excentrodendron tonkinense*), Ericaceae (*Rhododendron* spp.), Illiciaceae (*Illicium* spp.), Euphorbiaceae (*Pometia* spp., *Vernicia* spp.), Aceraceae (*Acer* spp.), Araliaceae (*Schefflera* spp.), Fagaceae (*Quecus* spp.), Poaceae, Asteraceae, Malpighiaceae and Oleaceae.
- Secondary evergreen forest on limestone is distributed in the transition zone between primary forest of the nearly pristine / core zone and degraded forest around Khau Ca. It is characterized by species including *Mallotus* spp., *Triadica rotundifolia* (Euphorbiaceae), *Pouzolzia* sp., *Elatostema* spp. (Urticaceae), *Pterospermum* spp., *Sterculia* spp. (Sterculiaceae), *Ficus* spp. (Moraceae), *Allocasia* spp. (Araceae), *Ophiorrhiza* spp. (Rubiaceae) and *Musa* spp. (Musaceae).

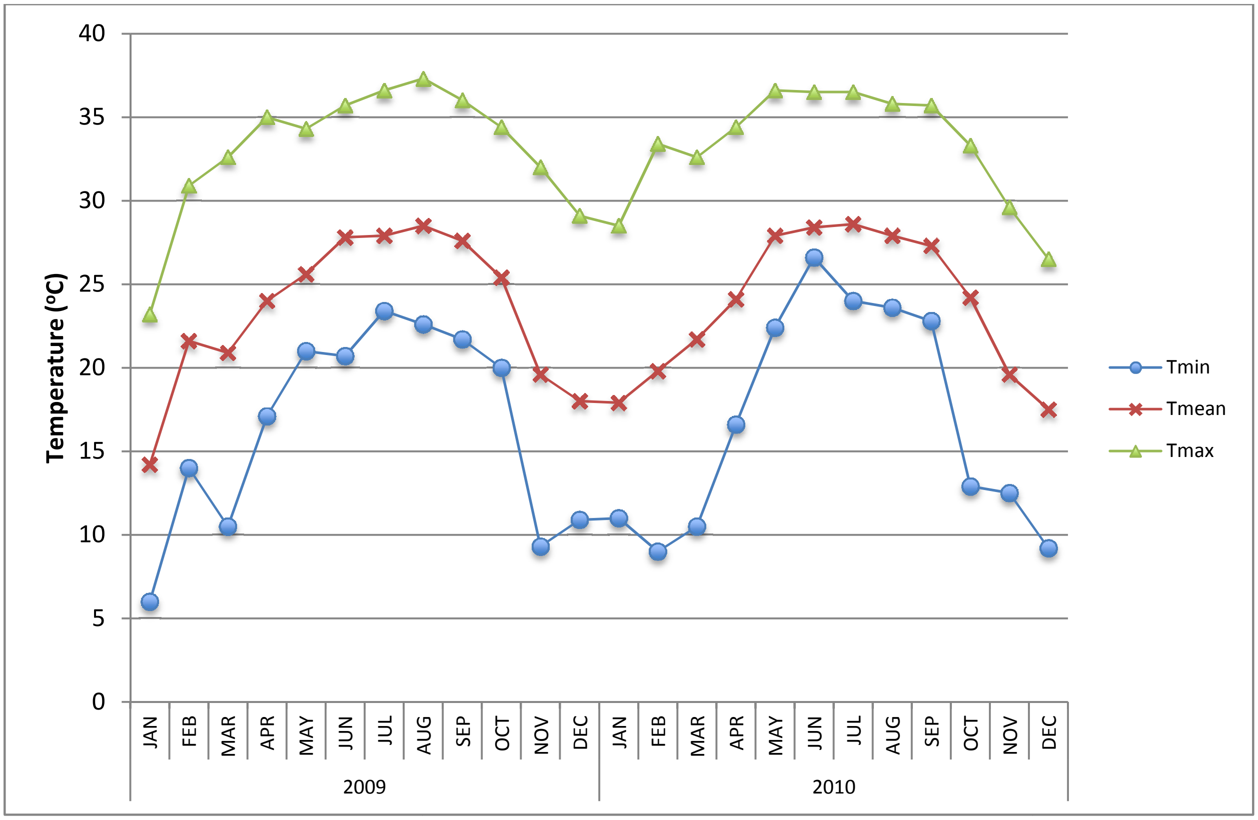

Figure 3.2. Temperature data for Khau Ca Forest recorded by Ha Giang Meteorological Station, January 2009 – December 2010

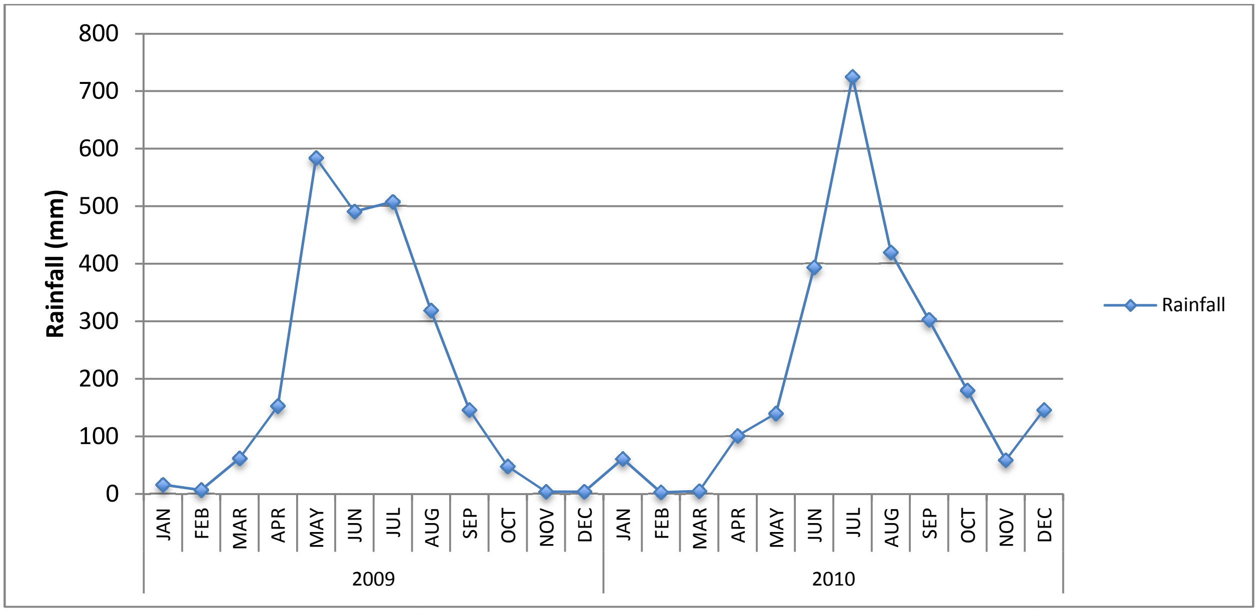

Figure 3.3. Rainfall data for Khau Ca Forest recorded by Ha Giang Meteorological Station, January 2009 – December 2010

- Secondary scrub ‘savannah’ occurs in areas rehabilitated from agricultural areas both inside and outside of the TSNM SHCA at Khau Ca. It is characterized by *Rubus alcaefolius*, *R. cochinchinensis* (Rosaceae), *Melastoma normale* (Melastomataceae), *Chromolaena odorata* (Asteraceae), *Thysanolaema maxima* (Poaceae), *Urena lobata* (Malvaceae), *Pteridium aquilinum* (Dennstaedtiaceae), *Mallotus* sp., *Macaranga* sp. (Euphorbiaceae), *Pouzolzia* sp. (Urticaceae), *Litsea* sp. (Lauraceae), *Thladiantha siamensis*, *Trichosanthes baviensis* (Cucurbitaceae), *Ipomoea* sp., *Merremia* sp. (Convolvulaceae), *Aralia armata* (Araliaceae) and *Iodes* spp. (Icacinaceae).
- Secondary grassland is primarily composed of the species *Imperata cylindrical* (Poaceae), *Euphorbia thymifolia* (Euphorbiaceae), *Plantago* spp. (Plantaginaceae), *Bidens pilosa* (Asteraceae), *Elephantopus scaber* and some unidentified species of the family Asteraceae.
- Cultivated vegetation occurs in the boundary of the TSNM SHCA at Khau Ca. It is dominated by crops of maize (*Zea mays*, Poaceae) as well as squash (*Cucurbita* spp., Cucurbitaceae) and other vegetables.

Nguyen Anh Duc *et al.* (2006a, 2006b), and Vu Anh Tai *et al.* (2009) recorded 471 vascular plant species belonging to 268 genera, 113 families and 4 phyla in this area. Rubiaceae and Orchidaceae are the most diverse families. Although the number of timber species is small, they constitute the largest populations and tallest trees in Khau Ca forest. These trees indicate floristic maturity and stability. This area is the prime habitat for *R. avunculus*. The most common tree species in Khau Ca forest are *Excentrodendron tonkinense* (Tiliaceae), *Garcinia* spp. (Clusiaceae), *Pometia pinnata* (Sapindaceae), *Diospyros* spp. (Ebenaceae), *Dendrocnide urentissima* (Urticaceae), *Bridelia balansae* (Euphorbiaceae), *Rhododendron* spp. (Ericaceae), *Illicium* spp. (Illiciaceae), *Vernicia* spp. (Euphorbiaceae), *Acer* spp. (Aceraceae), *Schefflera* spp. (Araliaceae), and *Quercus* sp. (Fagaceae). Threatened plants in Khau Ca forest with high priority for conservation include *Amentotaxus argotaenia*, *Excentrodendron tonkinense*, *Pinus* *kwangtungensis, Ardisia silvestris, Nageia fleuryi* and slippered orchids such as *Paphiopedilum hirsutissimum, P. malipoense, P.micranthum,* and *P. henryanum* (Nguyen Anh Duc *et al.*, 2006a, 2006b).

3.2.4. Faunal Richness

At least 33 mammal species have been recorded at TSNM SHCA at Khau Ca, belonging to 16 families and seven orders (Furey and Vuong Tan Tu, 2006; Le Khac Quyet and Luu Tuong Bach, 2006). *R. avunculus* is sympatric with four other primates including stump-tailed macaque (*Macaca arctoides*), Assamese macaque (*M. assamensis*), Bengal slow loris (*Nycticebus bengalensis*), and pygmy loris (*N. pygmaeus*) in Khau Ca (Le Khac Quyet and Luu Tuong Bach, 2006).

The bird community of Khau Ca Forest includes 153 species belonging to 26 families and is characteristic of forests on limestone in being composed of a large number of species of the families Megalaimidae and Sylviidae. The species most frequently recorded in this habitat include the great barbet (*Megalaima virens*), red-vented barbet (*M. lagrandieri*), golden-throated barbet (*M. franklinii*), streaked wren babbler (*Napothera brevicaudata*), eyebrowed wren babbler (*N. epilepidota*), slaty-bellied tesia (*Tesia olivea*), yellow-browed warbler (*Phylloscopus irnonatus*), white-spectacled warbler (*Seicercus affinis*), golden babbler (*Starchyris chrysaea*), grey-throated babbler (*S. nigriceps*), grey-cheeked fulvetta (*Alcippe morrisoni*), striated yuhina (*Yuhina castaniceps*), and white-bellied yuhina (*Y. zantholeuca*) (Le Manh Hung, 2006).

At least, two amphibian species and twelve reptile species have been recorded in the Khau Ca area (Le Khac Quyet and Luu Tuong Bach, 2006).

3.3. Selection of Study Site

Khau Ca Forest, which is the heart of the TSNM SHCA at Khau Ca (see Figure 3.1), contains over 100 individuals of *R. avunculus*, the largest remaining population for this species as noted above (Dong Thanh Hai, 2011; Le Khac Quyet and Covert, 2010; Hoang Van Tue, *pers. comm.*, 2013). Also, as noted above other populations of this critically endangered species in Na

Hang and Cham Chu Nature Reserves have shown recent declines due to hunting pressures, loss of habitat and habitat disturbance by human activities (Covert *et al.*, 2008; Dong Thanh Hai, 2011; Dong Thanh Hai *et al.*, 2006; Le Khac Quyet and Covert, 2010; Le Xuan Canh and Boonratana, 2006; Thach Mai Hoang, 2011). Covert *et al.* (2008) noted that Khau Ca is an ideal location to protect *R. avunculus* and to implement research and conservation programs.

3.4. Study Subjects

Following methods outlined in Williamson and Feistner (2003) from 2005 to present, we have been working on habituating *R. avunculus* in Khau Ca Forest. Four field assistants and I have followed *R. avunculus* troops at least five days a month. During follows we attempt to stay in contact with the primates without startling them or disrupting their behavior. At the moment, *R. avunculus* in Khau Ca are semi-habituated (i.e., they do not immediately flee when they encounter researchers and local assistants in camouflaged uniforms), permitting us to observe (at a distance of 20 – 50 m) and collect their positional behaviors an average of four hours a days for five days each month (about 20 hours per month).

Figure 3.4. Khau Ca Landscape

3.5. Forest Structure Data

3.5.1. Transect and Plot Setting

Four local research assistants and I have developed an approximately 20 km long trail system covering a large altitudinal gradient from approximately 640 m to 1,300 m a.m.s.l. through *R. avunculus*' day and home ranges in Khau Ca Forest since 2004 (Figure 3.1).

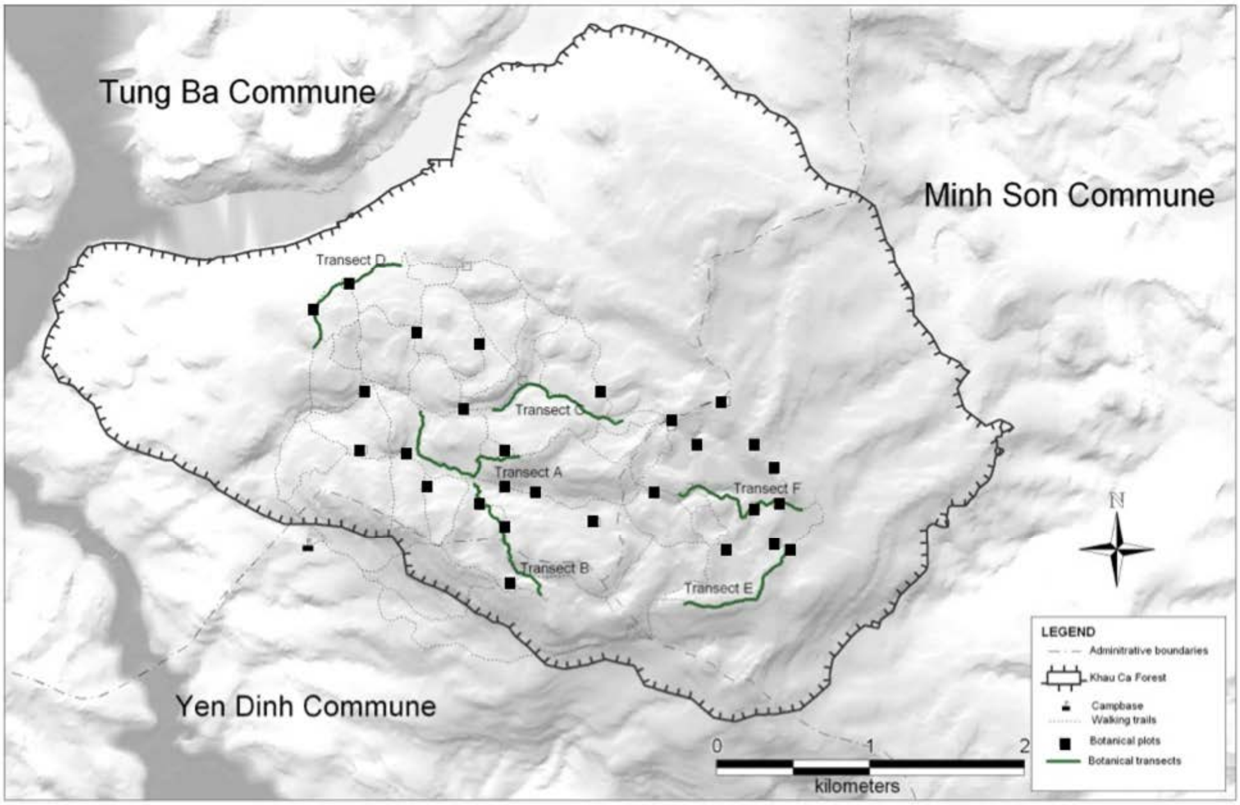

Figure 3.5. Map of trail system, phenological transects, and plots in Khau Ca Forest

We established six one kilometer long phenological transects with assistance of Dr. Barth Wright (Kansas City University of Medicine and Biosiences), and two botanists, Mr. Nguyen Anh Duc and Mr. Vu Anh Tai (Vietnam National University, Hanoi) in 2005 and 2008, each of which is four meters wide and was selected to cover both altitudinal and soil gradients (Figure 3.5). The six transects follow the established trails and did not require much foliage cutting, thus limiting and additional forest disturbance. As evidence of this, no trees over 5 cm of diameter at breast height (DBH) have been damaged in anyway by trail cutting. While these are not true transects (i.e. running in straight lines), they are treated as random sections of straight line transects, and with randomization and/or nonparametric statistical tests these data are analyzed for differences in species composition, tree density and diversity, forest structure, crop yield, and seasonal shifts in phenology. This method of phenological data collection was employed to permit local research assistants and I to simultaneously collect phenological data and census information bimonthly by walking the established trails.

Thirty 20-by-50 m plots have also been established in different ecoregions throughout the Khau Ca Forest. The data from these plots have been compared to those from transects. The sampling methods used in these plots follow standard methods established by botanists at Vietnam National University, Hanoi (VNUH) and provide a data set that can be directly compared to other studies conducted by VNUH researchers. The only addition to the established plot methods was the grade and direction of the plot slope.

3.5.2. Tree Measurement

Given the size of the trees in this forest and the large size of the study area we use a 10 cm diameter at breast height (DBH) cutoff for analysis (Husch, 1993). All trees of 10 cm DBH or larger were sampled within two meters of either side of six one-kilometer transects and within 30 plots. Aluminum tags were used to identify the trees and to mark the height at which DBH was measured.

Standard botanical data were collected including taxon, DBH, bole height, tree height, canopy shape, canopy diameters (both long and short), % leaf flush, % flower/inflorescence, % fruit, % horizontal substrates, % oblique substrates, % vertical substrates estimated within each tree crown, and associated climbers and epiphytes.

- **DBH** is measured in centimeters (cm) using a DBH measuring tape (Forestry Suppliers). In the case of multi-trunked trees DBH is measured and summed on all trunks with DBH

≥10 cm. Following Husch (1993) heavily buttressed trees were measured above the buttress, if possible.

- **Bole height** and total **tree height** (m) were measured and/or estimated in meters (m) based on 1.25 m stick at base and by using a rangefinder (Nikon Prostaff 5 rangefinder).

3.5.3. Tree Identification

Plant identification and classification were done in consultation with Mr. Nguyen Anh Duc, a VNUH botanist based on field observations and voucher samples. Tree family and species names and ID number were included on the tree tags.

3.5.4. Phenological Monitoring

Phenological monitoring was carried out bimonthly following Husch (1993) along six transects from August 2009 – July 2010. Each transect was walked and recorded twice a month on a rotating schedule. Data collection included relative abundance or absence of young leaves, unripe fruit, ripe fruit, and buds with flowers on trees within six transects.

3.6. Behavioral Data

3.6.1. Behavioral Data Collection

The physical structure of the Khau Ca primary forest, which is situated on a limestone substrate, impedes continuous follows of the semi-habituated *R. avunculus* making it difficult to follow focal animals on foot and record behavioral data at the same time. To assist in gathering and preserving data, handheld camcorders (i.e., harddrive and MiniDV cameras) were used to collect video segments of positional behavior of *R. avunculus*. Initially, field assistants and I conducted a two-month-pilot-study to determine the best ways to use the camera and their accessories, to practice filming techniques, and to test and correct videography methods. Subsequently, time was spent following the monkeys and gathering video data. Advantages of videography for behavioral studies have been noted by Rowe and Myers (2011) including lightweight, portable and easy to use for fieldwork, long term digital storage capacity, and permitting the playback of behaviors of interest (Lehner, 1996; Martin and Bateson, 1993). In particular, the use of a video camera allowed me to collect and quantify behaviors that include the movements which occur too quickly to be measured in real-time by direct observations.

In this study, data collection focused on adult, juvenile and infant *R. avunculus*. When a *R. avunculus* group was contacted a GPS reading of its location was taken and data collection was initiated on the first adult female or male observed as a focal animal that would be filmed continuously, until no longer in sight, and then the nearest neighboring animal would be chosen for filming. This method allows focal animal continuous sampling (Altmann, 1974; Martin and Bateson, 1993; Paterson, 2001) to be used when collecting behavioral data from the films. In total, 385 video hours of data were collected (187 hours in 2009 and 199 hours in 2010) (Appendix 1) and stored in original tapes (i.e., MiniDV tapes). When analyzed, all video data was digitally converted and stored on external harddrives, and displayed by a free and open source software, VCL media player for Mac (http://www.videolan.org/vlc/). Raw data of positional behavior and support use of *R. avunculus* were extracted (i.e., sampled) from the videos and entered into the Excel® spreadsheets on a monthly basis for further analyses and tests.

3.6.2. Sampling Methods Used in this Study

In this study, all positional behaviors were collected from these videos using bout sampling technique on focal animals (Fleagle, 1976a). The unit of observation was a positional sequence, which was composed of a series of locomotor and postural bouts. A locomotor bout occurred when an animal moved to displace its center of gravity by more than one body length. While an animal was moving, any change in gait, substrate size, or substrate orientation signaled a change of locomotor bout because locomotion is likely to differ on supports of different size or orientation. Postural bouts were scored when an animal is stationary or not displacing its center of gravity by more than one body length. Displacement of the center of gravity by less than one body length was classified as a shift in posture (Prost, 1965). The data collection techniques outlined above follows previously developed protocols by Bitty and McGraw (2007), Dagosto

(1994), Doran (1992a, 1993), Fleagle (1976a), Fleagle and Mittermeier (1980), Garber and Leigh (2001), Gebo and Chapman (1995a, 1995b, 2000), Guillot (2011), Hunt *et al.* (1996), McGraw (2000), Stevens *et al.* (2008), and Susman *et al.* (1980). Information collected at each bout includes:

1) **Time and length of a given behavior.**
2) **Sex –** Sex categories included Male, Female, and Unknown. Adult sex was relatively easy to determine using body mass and external genitalia. It was more difficult to determine the sex of infants and juveniles as external genitalia are not fully formed and/or visible.
3) **Age Determination:** Four developmental age categories are compared. These include five aging stages of infant, juvenile, subadult male and adult (Table 3.1).

Table 3.1. Sex and age categories of *R. avunculus* used in this study

Age/sex Categories	**Definitions**
Adult male	Largest members of group with robust head and large body, face skin bluish, lips pink and thick, throat orange, penis black, tail with curly fur and is much longer than body and head (Figure 3.6).
Adult female	Large individuals, body slimmer than adult male, face skin dark bluish to dark, nipples big and black, tail white with smooth fur (Figure 3.6).
Adult female with infant	Adult female carrying her infant (Figure 3.6).
Subadult male	Large male individuals, body size over two-thirds of adult male, tail long with furs less curly (Figure 3.7).
Juvenile 2	Medium-sized individuals, actively playing, orange patch on the throat less prominent, tail smooth with short furs (Figure 3.6).
Juvenile 1	Small-sized individuals, actively playing (Figure 3.6).
Infant	Smallest individuals, nursing, in contact with mother or alloparents, sex underdetermined, pelage white to grayish white, head and back grey to dark grey (Figure 3.6).

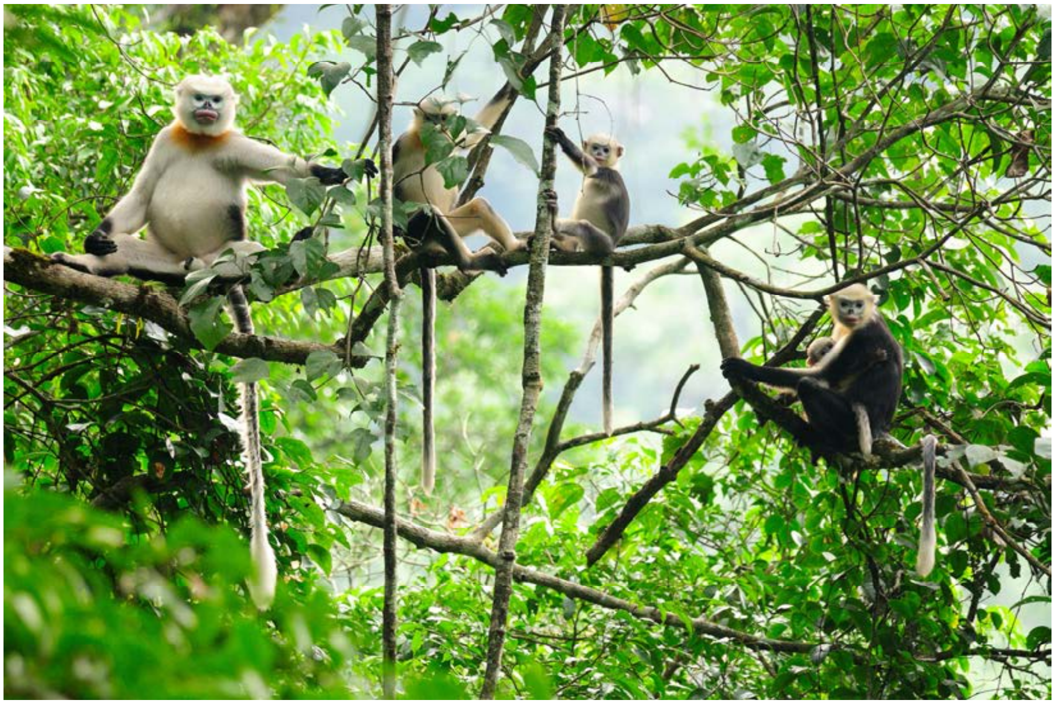

Figure 3.6. A group of the Tonkin snub-nosed monkeys (*R. avunculus*)
Left to right: Adult male, Juvenile 2, Juvenile 1, and Adult female and infant.

Figure 3.7. Subadult male *R. avunculus*

4) **Associated maintenance behaviors:**

- **Rest**: The focal animal had stopped for an extended period of time, usually in order to sleep or rest with no active behavior.
- **Travel**: The focal animal is moving (body mass is displaced) without feeding.
- **Feeding:** The focal animal was holding or processing a food item (ingestion).
- **Foraging**: The focal animal was actively searching for foods.**Social behaviors**: The focal animal was observed interacting with one or more group members. Subcategories include: vocalizing, grooming, playing, chasing, displaying, copulating, allomothering, fur rubbing, and fighting.
- **Display**: The focal animal is observed displaying at humans or other species (e.g., birds and macaques). Displays include facial expression and branch shaking or throwing.
- **Unknown behaviors**: the activity of focal animal could not be seen of uncategorized.

5) **Positional behaviors**: postural and locomotor modes expressed by *R. avunculus* in Khau Ca Forest as defined by Hunt *et al*. (1996) (see Table 3.2).

6) **Support size:** The diameter of the support(s) used by the focal animal was estimated in centimeters (cm). When a focal animal used more than one support, usually the supports were estimated approximately the same size. On the occasions when the supports were not the same size, the size of the support that supported the most animal’s weight was recorded. Prior to this particular study, I trained myself in estimating diameters by visual estimation of branch size at a distance followed by actual measurement. In addition, I visually assessed substrate size relative to the body size of the study subject. All support size categories used in this study are listed and defined in Table 3.3.

Table 3.2. Definition of postural and locomotor modes expressed by *R. avunculus* in Khau Ca Forest as defined by Hunt *et al*. (1996)

	Definition
Postural modes:	
Sit	“A posture in which the ischia bear substantial portion (usually more than half) of the body weight; the torso is relatively orthograde (|)” (p. 367). Submodes: *Sit-in*, *Sit-out, Foot-prop sit*, *Sit-in/out*, *Ischium-sit*, *Sit/forelimb-suspend*, and *Angled sit.*
Cling	“Flexed limb posture most common on vertical-subvertical supports” (p. 396). Submodes: *Unimanual cling*, and *Bimanual cling*.
Stand	- “*Quadrupedal stand*: Four-limbed standing on horizontal or subhorizontal supports; the elbow and knee are (relatively) extended and the trunk is near horizontal” (p. 371). - “*Crouch*: Quadrupedal flexed elbow and/or flexed knee posture” (p. 371).
Bipedal stand	- “*Flexed bipedal stand*: Standing on the hindlimbs with no significant support from any other body part. The torso is typically held at an approximately 45^{o} angle. The hip and knees are flexed” (p. 371) - “*Stand/forelimb-suspend*: More than half of the body weight supported by the hindlimbs, but there is significant support from a forelimb oriented in a forelimb-suspend pattern” (p. 371).
Forelimb-suspend (= arm-hang)	“Posture wherein more than half of the body weight is borne by the forelimb(s) grasping a support above the animal's center of mass” (p. 372). Submodes: *Unimanual forelimb-suspend*, and *Bimanual forelimb-suspend*.
Lie	“Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso” (p. 373). Submodes: *Lateral lie*, *Sit/lie*, *Sprawl*, and *Supine lie*.
Locomotor modes:	
Quadrupedal walk	“Locomotion on top of supports angled at $< 45^{o}$ typically all the four limbs contact the support in a particular sequence. The torso is pronograde (–) or roughly parallel to the support. Walking is distinguished from running principally by its slow or medium speed” (p. 375).
Bipedal walk	“*Flexed bipedal walk*: [The hindlimbs provide support and propulsion, with onlyinsignificant contributions from other body parts], …the hip and knee are relatively more flexed” (p. 377).
Bipedal hop	“Torso-orthograde (|) bipedal progression wherein the hindlimbs push off and land roughly simultaneously; there is a period of free flight (i.e. period of time in which no body part touches a support)” (p. 377).
Quadrupedal run	“Fast locomotion using asymmetrical or irregular gaits and with a period of free flight” (p. 377).
Vertical climb	- “*Flexed-elbow vertical climb*: Ascent on supports angled at $\geq 45^{o}$… The torso is held pronograde (|) and nearly parallel to the support being climbed. Grasping hands are almigrade in their contact with the support, and feet are semiplantigrade” (p. 378). - “*Ladder climb*: Similar to flexed-elbow climbing except supports are often relatively horizontal, and are never a single vertical support” (p. 379).

	- “*Vertical scramble*: Upward ($\geq 45^{o}$ progression on multiple often oddly angled supports, typically without a discernible gait pattern” (p. 379). - “*Pulse climb* (= vertical bound): Ascent of supports angled at $\geq 45^{o}$. The forelimbs grasp a support as the hindlimbs are gathered underneath the body by flexion of the knee, hip, and spine; extension of the hindlimbs and back push the body upward.” (p. 379). - “*Rump-first descent*: …rump-first descent, exception multiple supports with odd orientations and diameters” (p. 379).
Torso-orthograde suspensory locomotion	- “*Forelimb swing* (= armswing): Similar to brachiate (L9a) but with little trunk rotation” (p. 380).
Bridge	- “*Cautious pronograde bridge*: A torso-pronograde (–) gap-closing movement where the hands reach out to grasp a support on one side of a gap and cautiously pull the body across the open space with the feet retaining their grips until a secure position is established on the other side” (p. 380–1).
Leap	“Leaping is a gap-crossing movement in which the hindlimbs principally are used as propulsors. The flexed hindlimbs and flexed back are forcefully extended, often aided by the forelimbs” (p. 381). Submodes: *Pronograde leap*, *Pumping leap*, and *Vertical cling leap*.
Drop	“This mode differs from leaping in that takeoffs are initiated not by substantial muscle propulsion, but by falling after releasing a support.” (p. 381). Submodes: *Unimanual suspensory drop*, *Bimanual suspensory drop*, and *Quadrupedal drop*.

Table 3.3. Support size categories

Support size categories	**Definitions**
Trunk	Usually vertical, stout, primary member of the tree from the ground up to the first divergent branches.
Bough	Secondary elements that range 15 – 20 cm in diameter, large arboreal supports incapable of being grasped.
Branch	Tertiary supports that range 2 – 15 cm in diameter, small arboreal supports capable of being grasped.
Twig	Twigs and leaves associated with branches, flexible terminal branches that can be grasped but are too small to support body weight without deforming substantially.
Liana (=vine)	Flexible, rope-like supports anchored at a minimum of two ends.

7) **Support orientation:** The support orientation categories used in this study are listed and defined in Table 3.4.

Table 3.4. Support orientation categories

Support orientation categories	**Definitions**
Horizontal	Arboreal supports that ranged from $0^o – 15^o$ from precise horizontal plane
Oblique	Arboreal supports that ranged from $16^o – 74^o$ from precise horizontal plane
Vertical	Arboreal supports that ranged from $75^o – 90^o$ from precise horizontal plane
Terminal	Arboreal supports of thin flexible, small supports
Fork	A point of separation of two or more large branches

8) **Support flexibility –** Flexibility of supports used by *R. avunculus* are defined as those which deformed under the weight of the focal animal (Table 3.5).

Table 3.5. Support flexibility categories

Support flexibility categories	**Definitions**
Stable	Arboreal substrate(s) are not deflected by weight of the focal animal
Flexible	Arboreal substrate(s) are shaken or deflected by weight of the focal animal

9) **Number of supports used –** The number of supports used by the focal animal was recorded according to the following categories defined in Table 3.6.

Table 3.6. Categories of number of supports

Categories of number of supports	**Definitions**
Single	The focal animal was supported by one support
Combined	The focal animal was supported by one support with some minor help from one or two collateral supports
Multi	The focal animal was supported by 2 – 4 supports of identical characteristics
Network	The focal animal was supported by a complex network of supports

10) **Out of sight** (OS) – was the code used when the focal animal was not visible or was not sufficiently visible to determine which activity it was performing.

3.7. Data Analysis

Raw data were entered into data spreadsheets and stored on a computer (Apple® Macbook Pro laptop) and backed-up on an external harddrive. The data were analyzed using a standard statistical package of Microsoft® Excel:Mac 2011. Locomotor and postural behaviors were analyzed in the context of maintenance activities (feeding, foraging, travel, social behavior, etc.) to determine the importance of different positional behaviors to these activities. The positional behavior of *R. avunculus* was also summarized and compared in the form of frequencies of locomotor and postural bouts (without timing or distance association) given the nature of the research questions and sampling protocol. Analyses consisted of descriptive statistics, two sample comparisons of behaviors and substrate types between habitat types and individuals, and analyses of variance among sex and age classes. The nature of the behavioral data collection (lack of independence between positional behaviors) demands the use of non-parametric statistics. I followed previous researchers in using G-Tests of Independence to compare the number of bouts between age and sex classes, and across positional categories to identify the likelihood that row and column variables in contingency (i.e., frequency) tables are independent and are sometimes referred to as Row x Column (R x C) tests of independence (McKillup, 2012; Sokal and Rohlf, 2009). G-Tests had been used to compare populations in previous studies of primate positional behavior, e.g., Doran (1993), McGraw (1996a), and Youlatos (1998a, 1998b, 2002).

CHAPTER IV

KHAU CA FOREST STRUCTURE

4.1. Introduction

This chapter describes the forest structure, phenology, and species composition of the plant community in Khau Ca limestone area inhabited by *R. avunculus*. Data are primarily based on quantitative analysis undertaken in six one-kilometer transects and 30 20-by-50 m plots. These data provide a detailed description of the physical structure and floristic composition, and a full understanding of productivity of plant parts (new leaves, fruits and flowers) in relation to temperature, rainfall and seasonality in Khau Ca Forest. Discussions of forest structure, phenology, food availability and habitat capacity are presented at the end of this chapter. This subject matter is important for understanding the ecology of *R. avunculus* because it provides greater clarity about the species composition and phenology of the habitat that is maintained under protection for *R. avunculus* in the Khau Ca Forest. This also helps to understand how *R. avunculus* modifies behavior throughout the year in relationship to changes in their habitat.

4.2. Methods

This section outlines the statistical methodologies utilized for analysis of vegetation and phenology in this chapter. Chapter III details the protocols for all measurements made on trees, the locations of phenology transects, phenological monitoring, tree identifications, as well as the collection of temperature and rainfall data.

Basal area is the cross-sectional area of a tree at 1.25 m above ground (breast height). Basal area (BA) was calculated from diameter at breast height (DBH) using the Equation 4.1.

$$\mathrm{BA} = \pi\left(\frac{DBH}{2}\right)^2 \qquad \text{(Equation 4.1)}$$

Comparison of tree density between transects and plots were performed using the Chi-square Test. Comparison of tree heights between transects required values to be log transformed to fulfill assumptions of normality; they were then compared by a one-way analysis of variance (ANOVA) using the General Linear Model (GLM). Post-hoc tests for differences between transects were calculated using Bonferroni's correction. Comparisons between transects of tree basal area and DBH were performed using the Kruskal-Wallis Test. In order to avoid Type I error caused by multiple tests, significance was set at $\alpha = 0.05$.

Importance Value Indices (IVI) were calculated for all trees on the six transects and 30 plots to determine the relative dominance of each tree species within the habitat. IVI were calculated following (Blanc *et al.*, 2000), where the IVI is the sum of relative density D_i and relative basal area G_i, for species *i* on each transect, where the sum of all species' IVIs in one transect equals 200. The following equation was used:

$$IVI_i = D_i + G_i$$
$$D_i = (n_i / n) \times 100 \qquad \text{(Equation 4.2)}$$
$$G_i = (g_i i / g) \times 100$$

Species diversity was computed using Shannon's and Simpson's diversity indices. The Shannon Diversity Index was computed as $H' = \Sigma P_i \times \ln P_i$, where H' is the index of diversity, P_i is the importance value of a species *i* as a proportion of all species (Shannon, 1948). Simpson's Diversity Index was computed as $C = \Sigma P_i^2$ where C is the index number and P_i as defined above (Simpson, 1949).

Percentages of trees with presence of new leaves, flowers and fruits within six transects were calculated monthly and used for estimating forest productivity. Comparisons of relative degree of fruiting, flowering, new leaf production and deciduousness between transects and plots, and within transects were performed using Wilcoxon's test for matched pairs. Tests for correlation between phenophases and environmental variables were performed using *Spearman Rank Correlation Coefficient*.

All statistical analysis was performed with the statistical software packages of SPSS v19.0 for *Chi-square tests*, *Kruskal-Wallis tests*, *Wilcoxon's tests* and *ANOVA* or JMP Pro11 for descriptive statistics.

4.3. Results

4.3.1. Forest Structure

Tree Density

In total, 2,772 trees were counted in transects and plots, with an average of 513 stems/ha (Table 4.1). In terms of tree density, Transect B showed the highest density with 855 stems/ha, followed by Transect A with 853 stems/ha, and Transect C showed the lowest density with 388 stems/ha (Table 4.1). Tree density was significantly different across the six transects and 30 plots plots ($\chi^2 = 42.27$, df = 1, $p < 0.001$) and between transects ($\chi^2 = 123.39$, df = 5, p < 0.001).

Table 4.1. Mean of tree height, DBH, basal area, and density for trees from six transects and 30 plots

	Tree height (m)	DBH (cm)	Total basal area (m^2)	Density (stems/ha)
Total 6 transects (n = 1,567)	**11.5 ± 4.9**	**27.1 ± 22.7**	**128.96**	**653**
Transect A (n = 341)	11.9 ± 5.9	28.9 ± 24.6	31.73	853
Transect B (n = 342)	10.4 ± 3.8	25.8 ± 21.0	24.60	855
Transect C (n = 155)	14.9 ± 6.4	32.8 ± 30.4	23.80	388
Transect D (n = 235)	10.7 ± 3.4	27.4 ± 20.0	17.85	588
Transect E (n = 306)	9.6 ± 2.4	19.0 ± 14.0	7.61	765
Transect F (n = 188)	14.5 ± 5.3	34.4 ± 25.4	23.37	470
Total 30 plots (n = 1,205)	**17.3 ± 7.5**	**28.5 ± 23.4**	**117.30**	**402**
TOTAL (plots + transects)	**14.0 ± 6.8**	**27.7 ± 23.0**	**246.26**	**513**

Tree Height

Mean tree height was 14.0 ± 6.8 m for the combined sample plot and transect data sets; 69.2% of trees were shorter than 15 m and only 8.9 % of trees were taller than 25 m. The maximum tree height was 50 m.

Mean tree height was 11.5 ± 4.9 m for the transects, and 17.3 ± 7.5 m for the plots. Mean tree height for Transect A was 11.9 ± 5.9 m, 10.4 ± 3.8m for Transect B, 14.9 ± 6.4 m for Transect C, 10.7 ± 3.4 m for Transect D, 9.6 ± 2.4 m for Transect E, and 14.5 ± 5.3 m for Transect F (Table 4.1; Figure 4.1).

Of the five tallest trees in all sampled plots and transects, Plot 9 contained one, and Plots 10 and 12 each contained two. The tallest trees were specimens of *Excentrodendron tonkinense* (n = 3) and *Diospyros* sp. (n = 2). There are 150 (3.8%) trees over 30 m.

Tree heights, log transformed, of transects and plots were compared using a one-way ANOVA (GLM) to determine whether all transects and plots were relatively homogenous in this aspect. This showed that height of trees from transects and plots were significantly different ($F = 618.55$, $df = 1, 2772$, $p < 0.001$, $n_{plots} = 1{,}205$, $n_{transects} = 1{,}567$).

Tree heights were also significantly different between transects ($F = 14.92$, $df = 5, 1567$, $p < 0.001$, $n_{transect\ A} = 341$, $n_{transect\ B} = 342$, $n_{transect\ C} = 155$, $n_{transect\ D} = 235$, $n_{transect\ E} = 306$, $n_{transect\ F} = 188$) (Figure 4.3). A post-hoc test using Bonferroni's correction showed that Transect A was not significantly different from Transects B, C, D and F ($p > 0.5$), and Transect E had significantly shorter trees than other transects ($p < 0.001$) (Table 4.2).

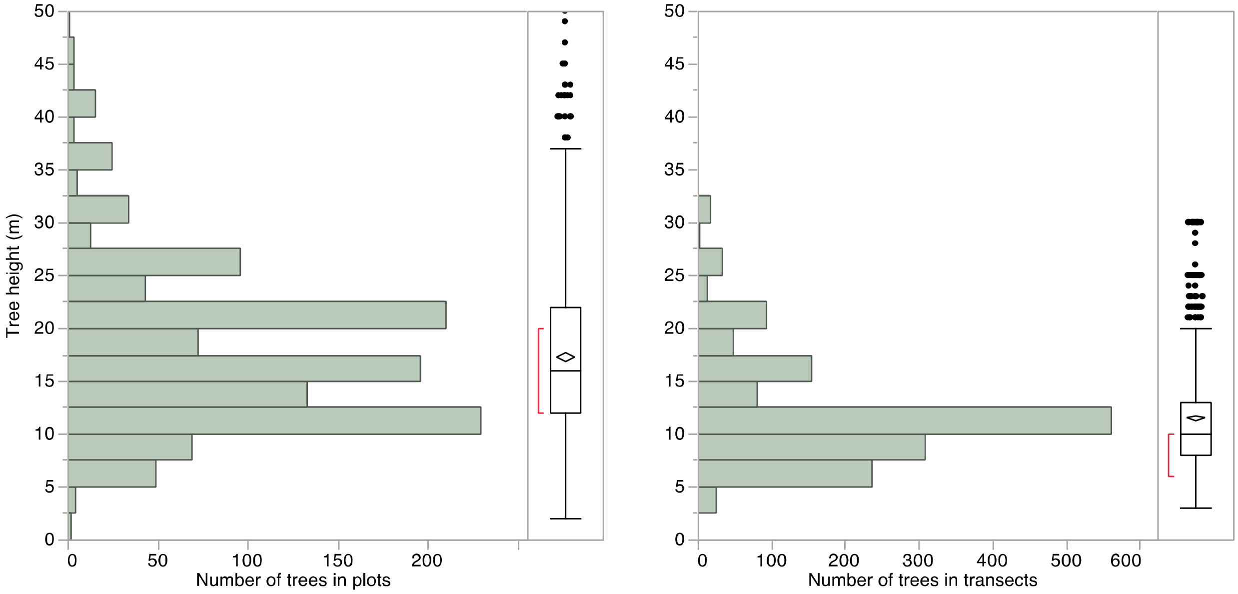

Figure 4.1. Distribution of tree heights by plots and transects

Note. Tree height: 30 plots (n = 1,205; 14.0 ± 6.8 m), 6 transects (n = 1,567, 11.5 ± 4.9 m)

Table 4.2. Post-hoc test using Bonferroni's correction for the transects

		Mean Difference	**Std. Error**	p value
Transect A	Transect B	3.11	1.70	1.000
	Transect C	-3.91	2.16	1.000
	Transect D	1.51	1.89	1.000
	Transect E	9.90	1.75	**0.000 *** **
	Transect F	-5.51	2.02	0.097
Transect B	Transect C	-7.03	2.15	**0.017 * **
	Transect D	-1.60	1.89	1.000
	Transect E	6.79	1.75	**0.002 ** **
	Transect F	-8.63	2.02	**0.000 *** **
Transect C	Transect D	5.43	2.30	0.278
	Transect E	13.82	2.19	**0.000 *** **
	Transect F	-1.60	2.41	1.000
Transect D	Transect E	8.40	1.93	0.**000 *** **
	Transect F	-7.03	2.18	**0.019 * **
Transect E	Transect F	-15.42	2.07	**0.000 *** **

Note. n.s.: not significant, * p < 0.05, ** p , 0.01, *** p < 0.001.

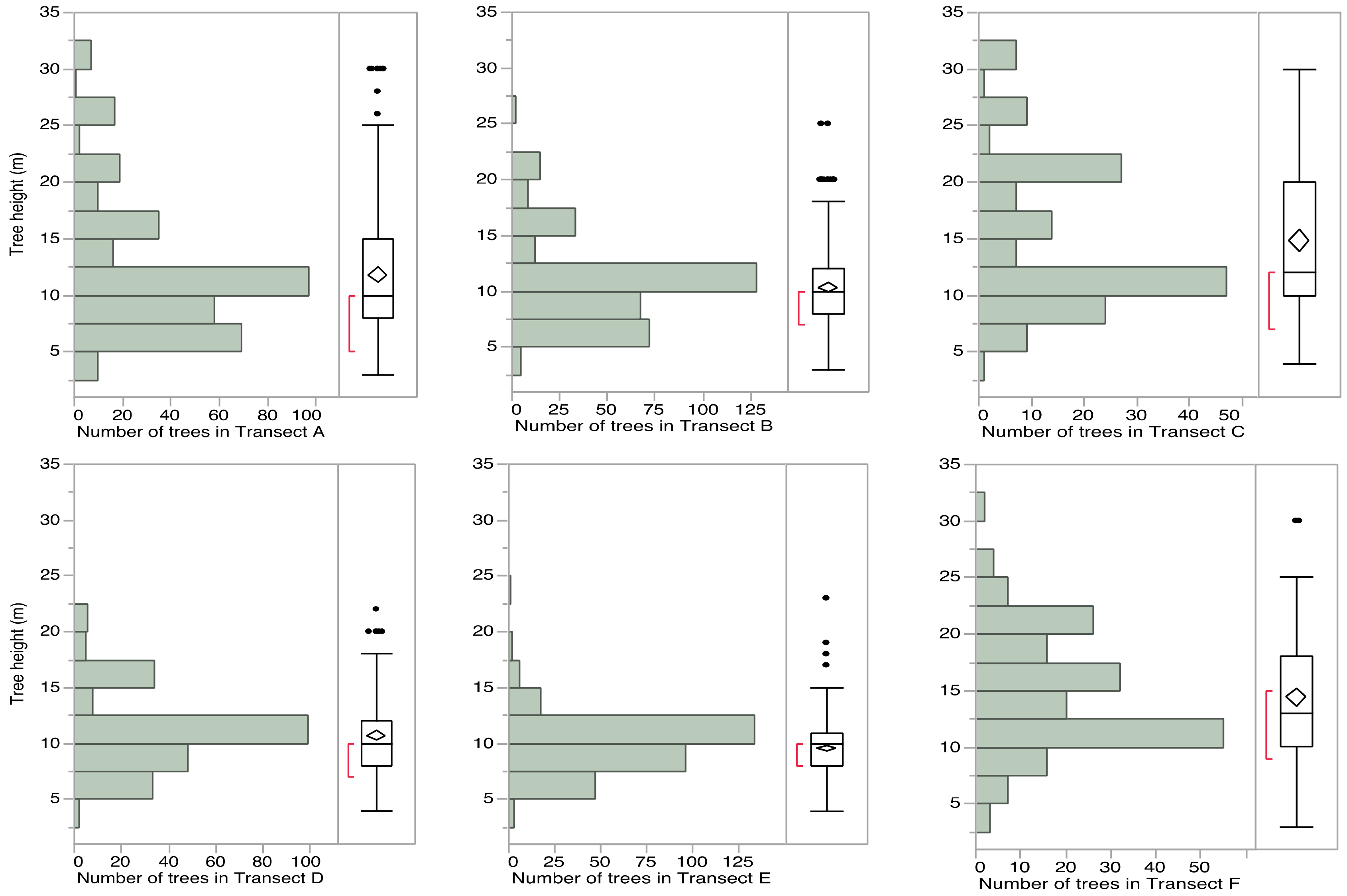

Figure 4.2. Distribution of tree height across the transects

Note. Tree height: Transect A (n = 314, 11.9 ± 5.9 m) Transect B (n = 342, 10.4 ± 3.8 m), Transect C (n = 155, 14.9 ± 6.4 m), Trasect D (n = 35, 10.7 ± 3.4 m), Transect E (n = 306, 9.6 ± 2.4 m) and Transect F (n = 188, 14.5 ± 5.3 m)

Diameter at Breast Height (DBH)

Mean DBH was 27.7 ± 23.0 cm for the whole sample (plots and transects); 70.8 % of trees have a DBH less than 30 cm and only 5.1 % of trees have a DBH greater than 70 cm. The maximum BDH was 205 cm (Table 4.1). Mean DBH for the trees of transects was 27.1 ± 22.7 cm, and 28.5 ± 23.4 m for plots (Table 4.1, Figure 4.3). Mean DBH was found to be significantly different between total transects and plots (χ^2 = 14.27, df = 1, $p < 0.001$, n_{plots} = 1,205, $n_{transects}$ = 1,567, Kruskal-Wallis Test).

Mean DBH was 28.9 ± 24.6 cm for Transect A, 25.8 ± 21.0 cm for Transect B, 32.8 ± 30.4 cm for Transect C, 27.4 ± 20.0 cm for Transect D, 19.0 ± 14.0 cm for Transect E, and 34.4 ± 25.4 cm for Transect F (Table 4.1, Figure 4.4). Mean DBH was found to be significantly different between transects (χ^2 = 120.50, df = 5, $p < 0.001$, $n_{transect\ A}$ = 341, $n_{transect\ B}$ = 342, $n_{transect\ C}$ = 155, $n_{transect\ D}$ = 235, $n_{transect\ E}$ = 306, $n_{transect\ F}$ = 188, Kruskal-Wallis Test).

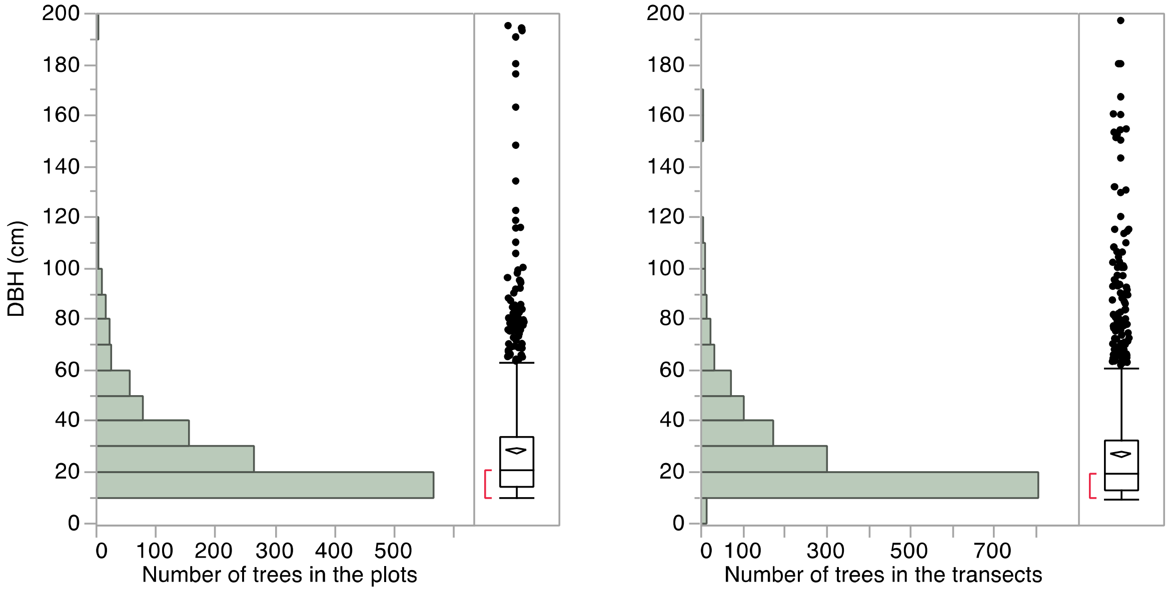

Figure 4.3. Distribution of DBH by plots and transects
Note. DBH: 30 plots (n = 1,205; 28.5 ± 23.4 m), 6 transects (n = 1,567, 27.1 ± 22.7 cm)

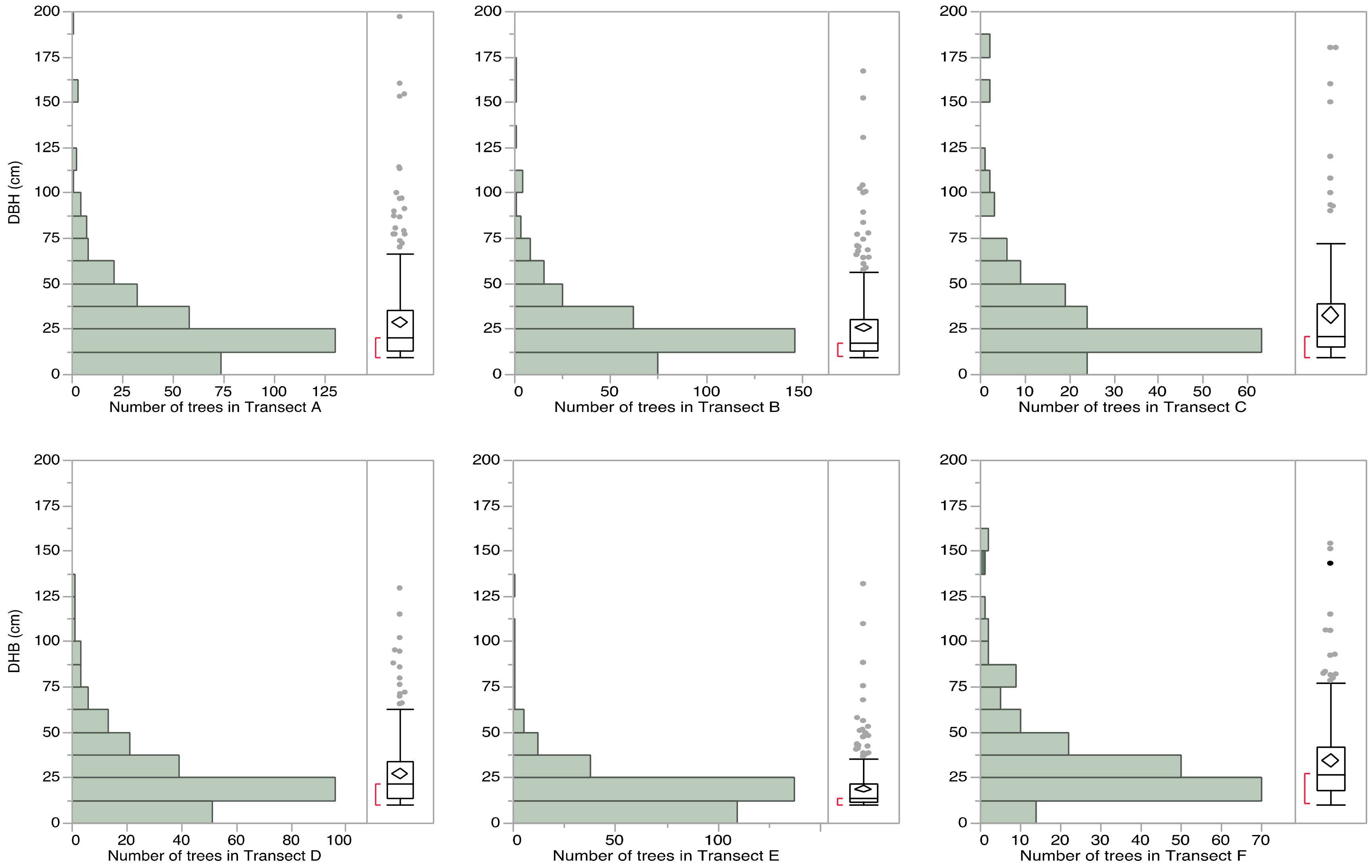

Figure 4.4. Distribution of tree at diameter at breast (DBH) across the transects

Note. DBH: Transect A (n = 314, 28.9 ± 24.6 cm) Transect B (n = 342, 25.8 ± 21.0 cm), Transect C (n = 155, 32.8 ± 30.4 cm), Trasect D (n = 35, 27.4 ± 20.0 cm), Transect E (n = 306, 19.0 ± 14.0 cm) and Transect F (n = 188, 34.4 ± 25.4 cm)

Of the five trees with the largest DBH in all sampled plots and transects, one was in Transect A, and one each in Plots 3, 5, 6, and 9. The largest trees were specimens of *Excentrodendron tonkinense* (n = 4) and *Pometia pinnata* (n = 1). There were 50 (02%) trees with DBH greater than 100 cm.

Basal Area

Total basal area for all sample transects and plots was 246.26 m^2 (45.60 m^2/ha); 80.1% of trees had basal areas under 0.1 m^2 and only 9.0% of trees had basal areas greater 0.25 m^2.

Total basal area of six transects was 128.96 m^2 (53.73 m^2/ha), and 117.30 m^2 for the plots (39.10 m^2/ha) (Table 4.1, Figure 4.5). Mean DBH was not found to be significantly different between transects ($\chi^2 = 24.66$, df = 1, $p < 0.001$, $n_{plots} = 1{,}205$, $n_{transects} = 1{,}567$, Kruskal-Wallis Test). Total basal area for Transect A was 31.73 m^2, 24.60 for Transect B, 23.80 m^2 for Transect C, 17.85 m^2 for Transect D, 7.61 m^2 for Transect E, and 23.37 m^2 for Transect F (Table 4.1, Figure 4.6). Mean DBH was found to be significantly different between transects ($\chi^2 = 153.07$, df = 5, $p < 0.001$, $n_{transect\ A} = 341$, $n_{transect\ B} = 342$, $n_{transect\ C} = 155$, $n_{transect\ D} = 235$, $n_{transect\ E} = 306$, $n_{transect\ F} = 188$, Kruskal-Wallis Test).

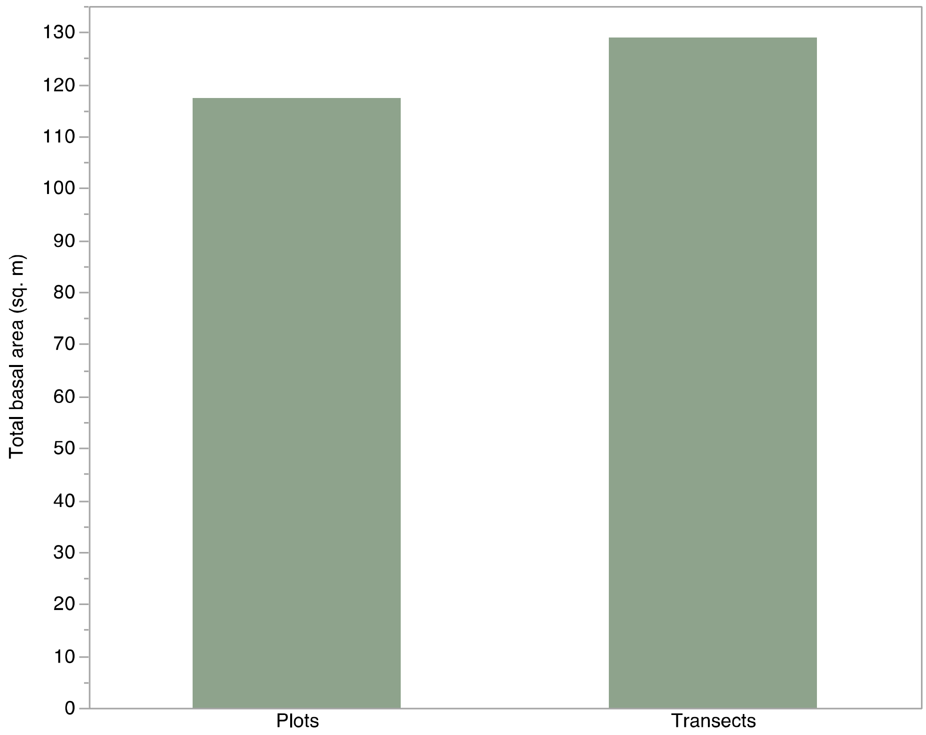

Figure 4.5. Total basal area by transects and plots

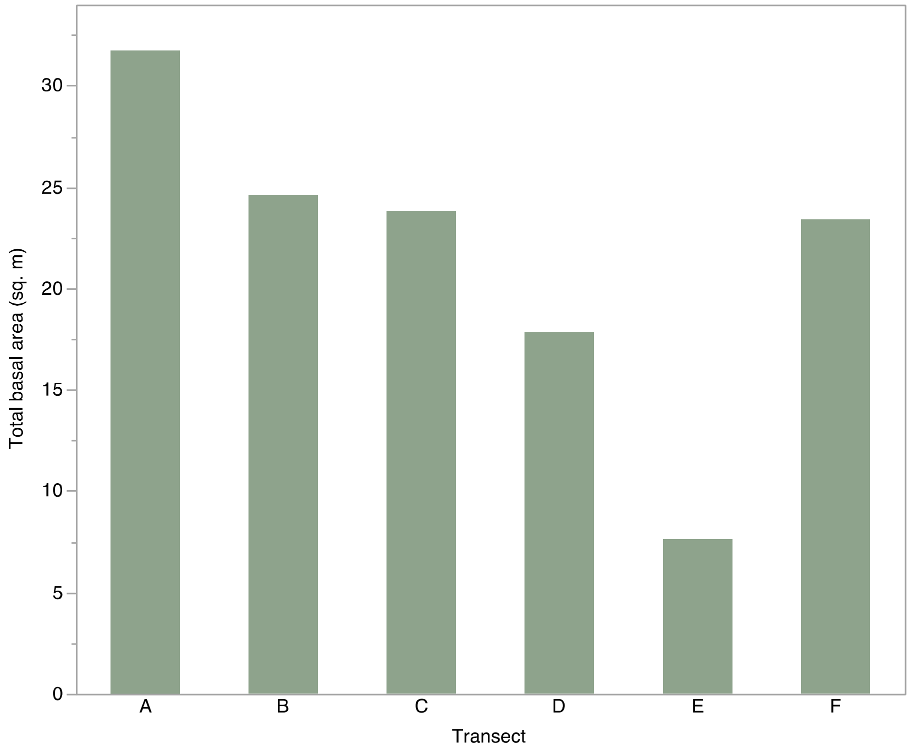

Figure 4.6. Total basal area across transects

Mortality and Tree Falls

During 12-month monitoring, there was some mortality and damage to trees in the transects primarily due to heavy wind. Thirty-two trees died during the period from August 2009 to July 2010, or 2.66% of all transect trees, with an annual death rate of 13 trees/ha/year (Table 4.3, Figure 4.7).

Table 4.3. Mortality of trees in six transects from August 2009 to July 2010

	Transect						
Month-Year	A	B	C	D	E	F	**Total**
Aug-09	0	0	0	0	0	0	0
Sep-09	0	0	0	0	0	1	1
Oct-09	0	0	0	0	0	1	1
Nov-09	0	0	0	3	0	1	4
Dec-09	0	1	0	3	1	2	7
Jan-10	3	1	0	3	2	3	12
Feb-10	3	4	0	3	1	3	14
Mar-10	3	6	0	3	2	3	17
Apr-10	3	9	0	6	2	4	24
May-10	4	9	0	6	2	5	26
Jun-10	5	9	0	6	2	5	27
Jul-10	6	12	0	7	2	5	32

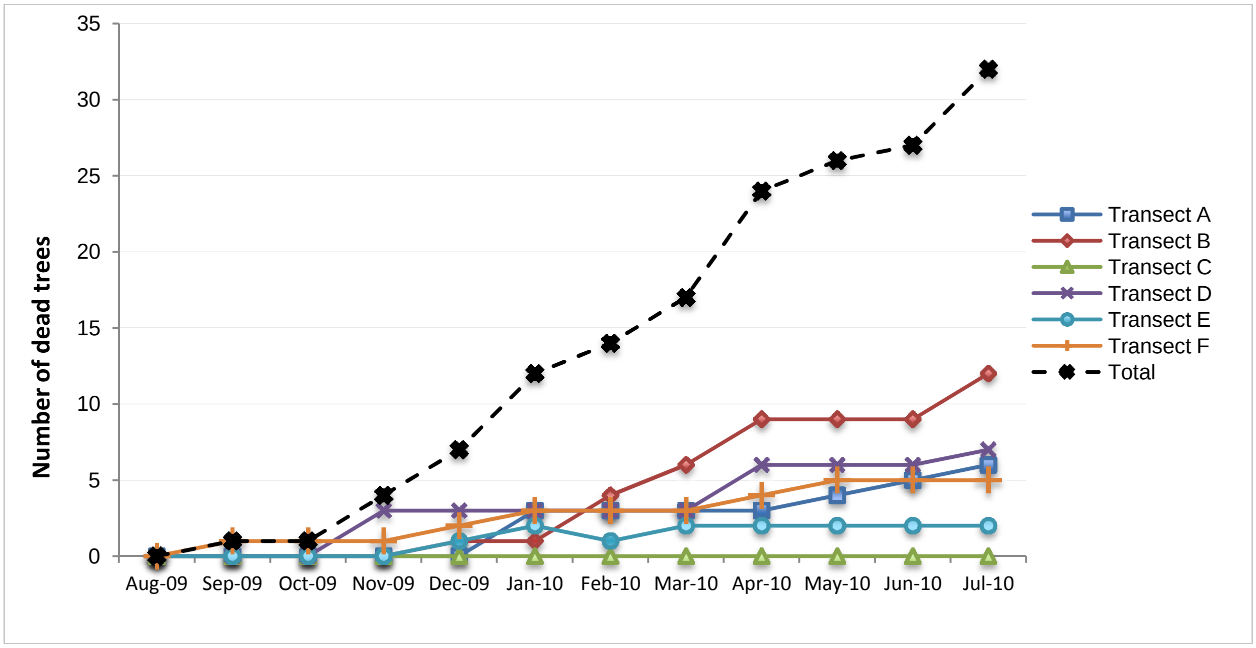

Figure 4.7. Cumulative mortality of trees in six transects from August 2009 to July 2010

4.3.2. Forest Productivity

Flowering Cycles

Patterns in flowering for six transects over 12 months are shown in Figure 4.8. Overall, Transect A averaged 2.39 % ± 3.79 of trees flowering each month, 4.08 % ± 4.18 in Transect B, 3.60 % ± 3.55 in Transect C, 1.26 % ± 1.18 in Transect D, 5.59 % ± 7.52 in Transect E and 6.75 % ± 8.94 in Transect F. Transects appear to be significantly different in frequency of flowering trees by month and significant difference between them in flower production was found (χ^2 = 15.07, df = 5, n = 12, p = 0.01, Wilcoxon Matched Pairs Signed Rank Test), and the Kendall's coefficient of concordance of 0.25 indicated fairly strong differences among the transects. Peak production occurred in March through May in 2010. The environmental variables of rainfall and temperature were found not to be significantly correlated to flowering activity (Table 4.4).

Table 4.4. Spearman Rank Correlation Coefficient matrix for phenophases and environmental variables

		Fruits	New leaves	Rainfall (mm)	Mean Temperature (^{o}C)
Flowers	Correlation Coefficient	- 0.378 n.s.	**0.818****	0.238 n.s.	0.238 n.s.
	Sig. (2-tailed)	0.226	**0.001**	0.457	0.456
	n	12	12	12	12
Fruits	Correlation Coefficient		0.063 n.s.	**0.741****	**0.729****
	Sig. (2-tailed)		0.846	**0.006**	**0.007**
	n		12	12	12
New leaves	Correlation Coefficient			**0.573** *	**0.648***
	Sig. (2-tailed)			**0.051**	**0.023**
	n			12	12

Note. n.s.: not significant, * p < 0.05, ** p < 0.01.

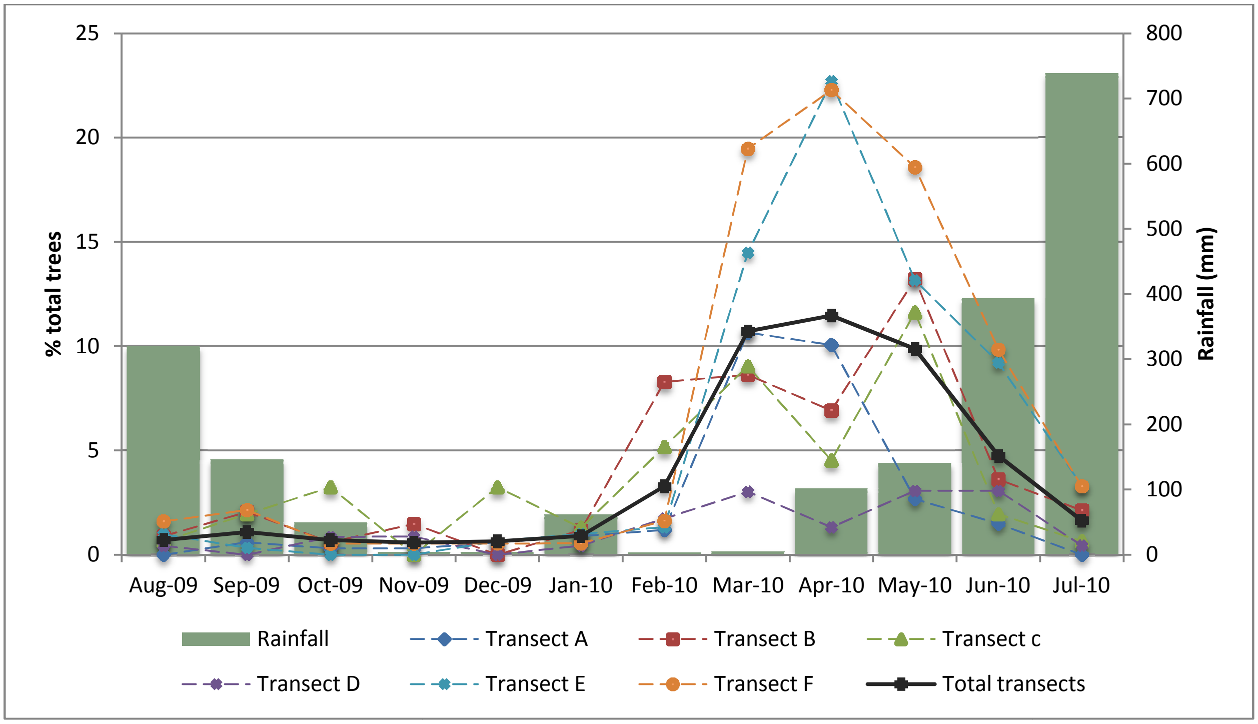

Figure 4.8. Monthly percentage of trees with flowers from transects with associated rainfall

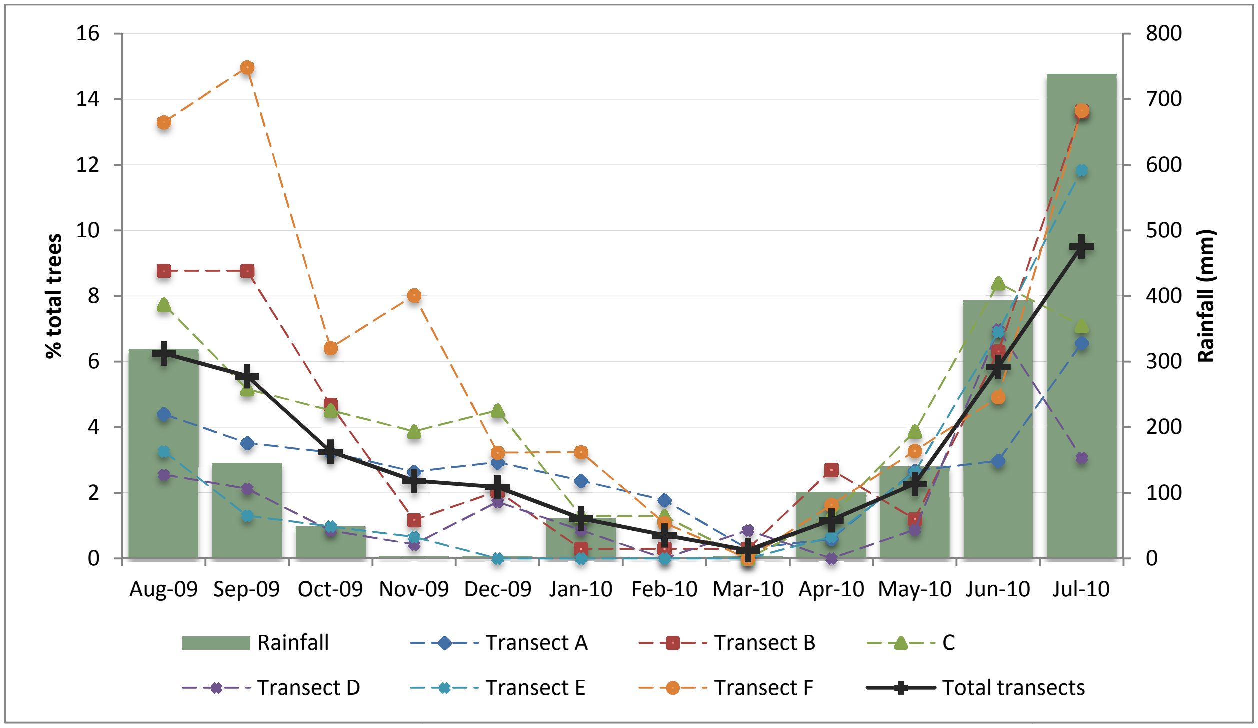

Figure 4.9. Monthly percentage of trees with fruits from transects with associated rainfall

Fruiting Cycles

Patterns in fruiting for six transects over 12 months are shown in Figure 4.9. Overall, Transect A averaged 2.83 % ± 1.65 of trees fruiting each month, 4.18 % ± 4.33 in Transect B, 4.09 % ± 2.74 in Transect C, 1.70 % ± 1.93 in Transect D, 2.35 % ± 3.60 in Transect E and 6.15 % ± 5.22 in Transect F. Transects appear to be significantly different in frequency of fruiting trees by month and significant difference between them in flower production was found (χ^2 = 22.86, df = 5, n = 12, p < 0.001, Wilcoxon Matched Pairs Signed Rank Test), and the Kendall's coefficient of concordance of 0.38 indicated fairly strong differences among the transects. Peak production occurred in June through September in 2010. The correlation between fruiting trees and environmental variables was positively significant (r_S = 0.7, p=0.006) (Table 4.4).

Leafing Cycles

Patterns in leafing for six transects over 12 months are shown in Figure 4.10. Overall, Transect A averaged 24.60 % ± 15.83 of trees leafing each month, 22.29 % ± 14.34 in Transect B, 29.41 % ± 17.76 in Transect C, 22.85 % ± 16.20 in Transect D, 20.82 % ± 18.91 in Transect E and 24.56 % ± 19.68 in Transect F. Transects appear to be significantly different in frequency of leafing trees by month and significant difference between them in flower production was found (χ^2 = 12.14, df = 5, n = 12, p = 0.03, Wilcoxon Matched Pairs Signed Rank Test), and the Kendall's coefficient of concordance of 0.20 indicated fairly strong differences among the transects. Peak production occurred in April through August in 2010. The correlation between trees with new leaves and temperature (r_S = 0.65, p=0.02) and rainfall (r_S = 0.57, p=0.051) was positively significant (Table 4.4).

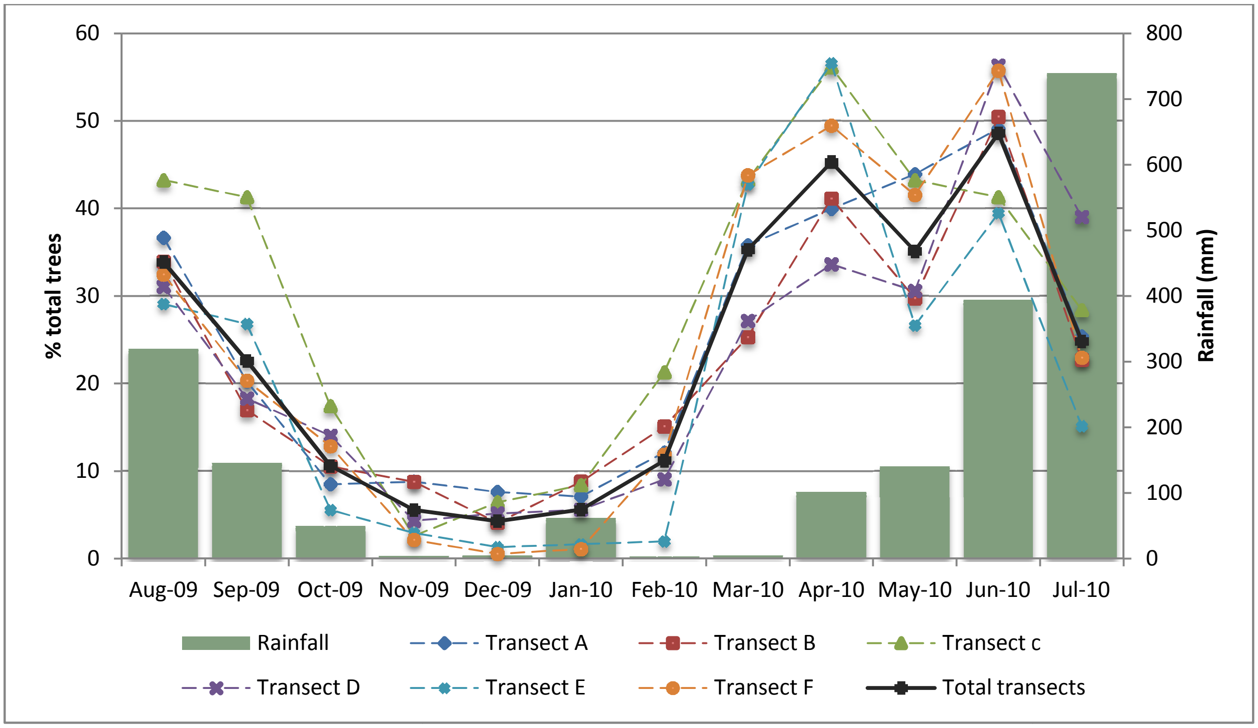

Figure 4.10. Monthly percentage of trees with new leaves from transects with associated rainfall

4.3.3. Species Richness and Diversity

Of the 2,772 trees of DBH ≥ 10 cm on six transects and 30 plots, a total of 109 identified species and 73 unidentified species belonging to 123 genera and 57 families were identified (Table 4.5, Appendix 2). The top ten most abundant tree families, genera, and species are presented in Table 4.6.

Table 4.5. Characteristics of tree resources in Khau Ca Forest

Parameter	**Values**		
	Transects	Plots	Transects + Plots
Richness (Total number of species)	144	119	182
Total of stems with BDH ≥ 10 cm	1,567	1,205	2,772
Density (stems/ha)	653	402	513
Shannon-Wiener's Index	4.21	4.06	4.33
Simpson's Index	0.02	0.03	0.02

The incidence of new species by plots was cumulated to determine whether plots had captured a significant proportion of the botanical diversity at the site (Figure 4.11).

The Shannon-Wiener Index of diversity (H') is 4.33 indicating thin Khau Ca Forest has relatively high species diversity (Table 4.5). Species noted to have contributed to high species diversity include: *Olea* sp. (0.19), *Polyalthia cerasoides* (0.18), *Polyalthia thorelii* (0.12), *Garcinia bracteata* (0.11), *Excentrodendron tonkinense* (0.11), and *Phoebe kunstleri* (0.10).

Importance Value Indices (IVI) were calculated for all species by transects and plots, with results presented in Figure 4.12. In this index, the higher the value, the more dominant the tree species is in the environment. It can be seen that *Polyalthia cerasoides*, *Olea* sp., and *Excentrodendron tonkinense* are the most dominant taxa in Khau Ca Forest, with over 10% of IVI values on transects and plots. IVI rank orders for the top 30 tree species are not statistically different between transects and plots ($r_s = 0.09$, p = 0.63, n = 30).

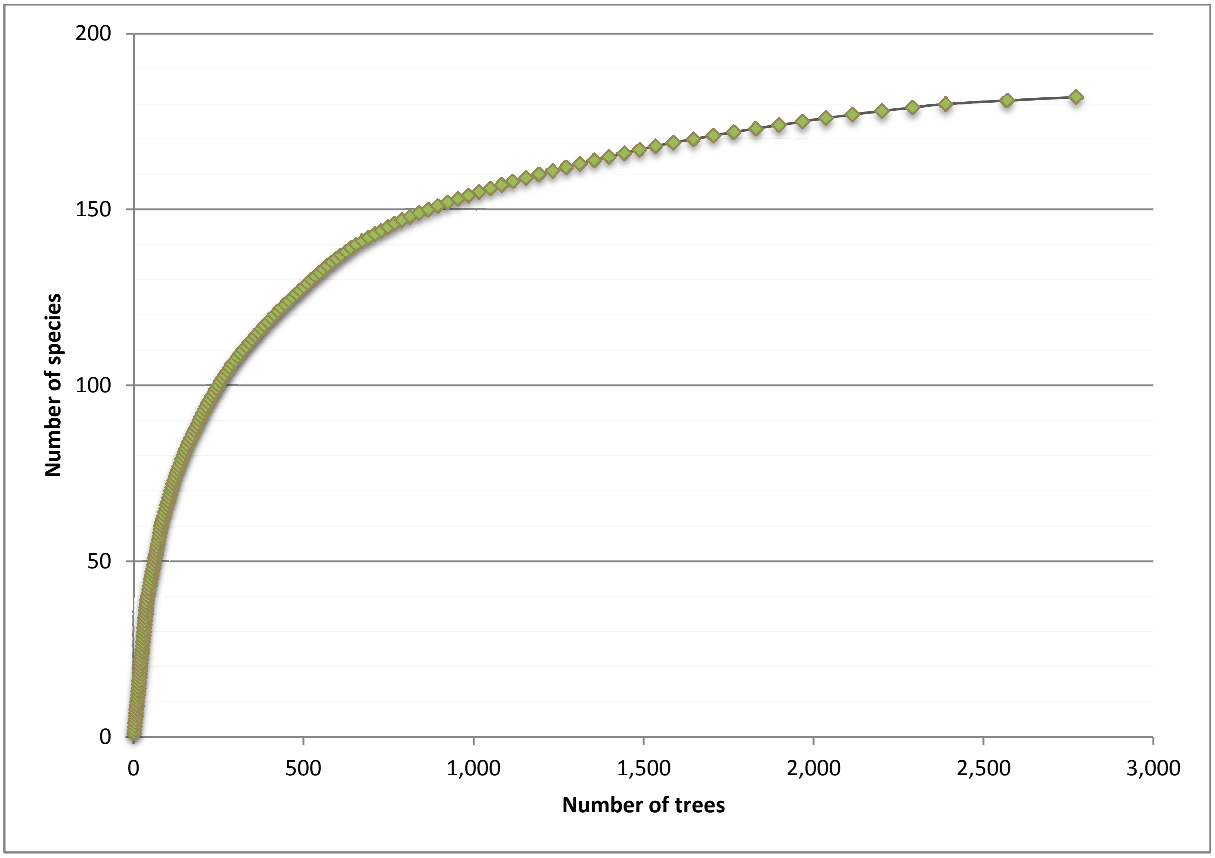

Figure 4.11. Species incidence curve for transect and plots combined

Table 4.6. Top ten tree families, genera, and species in Khau Ca Forest

Transects	***n***	**Plots**	***n***	**Transects + Plots**	***n***
Top 10 families					
Annonaceae	185	Annonaceae	188	Annonaceae	373
Lauraceae	147	Lauraceae	133	Lauraceae	280
Oleaceae	118	Oleaceae	96	Oleaceae	214
Euphorbiaceae	117	Clusiaceae	83	Euphorbiaceae	190
Fagaceae	102	Euphorbiaceae	73	Clusiaceae	170
Clusiaceae	87	Ulmaceae	61	Fagaceae	133
Aceraceae	57	Meliaceae	52	Sapindaceae	105
Sapindaceae	56	Sapindaceae	49	Ulmaceae	105
Tiliaceae	50	Myrtaceae	45	Meliaceae	101
Meliaceae	49	Ebenaceae	42	Tiliaceae	87
Top 10 genera					
Polyalthia	168	*Polyalthia*	144	*Polyalthia*	312
Olea	107	*Olea*	96	*Olea*	203
Garcinia	74	*Garcinia*	75	*Garcinia*	149
Vernicia	68	*Phoebe*	65	*Phoebe*	121
Acer	57	*Celtis*	61	*Celtis*	105
Phoebe	56	*Machilus*	46	*Excentrodendron*	87
Castanopsis	50	*Syzygium*	45	*Acer*	81
Excentrodendron	50	*Diospyros*	42	*Sapindus*	75
Celastrus	46	*Excentrodendron*	37	*Machilus*	71
Celtis	44	*Sapindus*	36	*Antidesma*	70
Top 10 species					
Polyalthia cerasoides	117	*Olea* sp.	96	*Olea* sp.	203
Olea sp.	107	*Polyalthia cerasoides*	64	*Polyalthia cerasoides*	181
Vernicia montana	67	*Polyalthia thorelii*	59	*Polyalthia thorelii*	97
Phoebe kunstleri	53	*Garcinia bracteata*	54	*Garcinia bracteata*	90
Castanopsis sp.	50	*Celtis japonica*	48	*Excentrodendron tonkinense*	87
Excentrodendron tonkinense	50	*Machilus platycarpa*	44	*Phoebe kunstleri*	78
Celastrus sp.	46	*Phoebe* sp.	40	*Celtis japonica*	69
Gmelina sp.	41	*Diospyros* sp.	39	*Vernicia montana*	69
Platycarya strobilacea	38	*Excentrodendron tonkinense*	37	*Aglaia* sp.	68
Polyalthia thorelii	38	*Aglaia* sp.	33	*Castanopsis* sp.	65

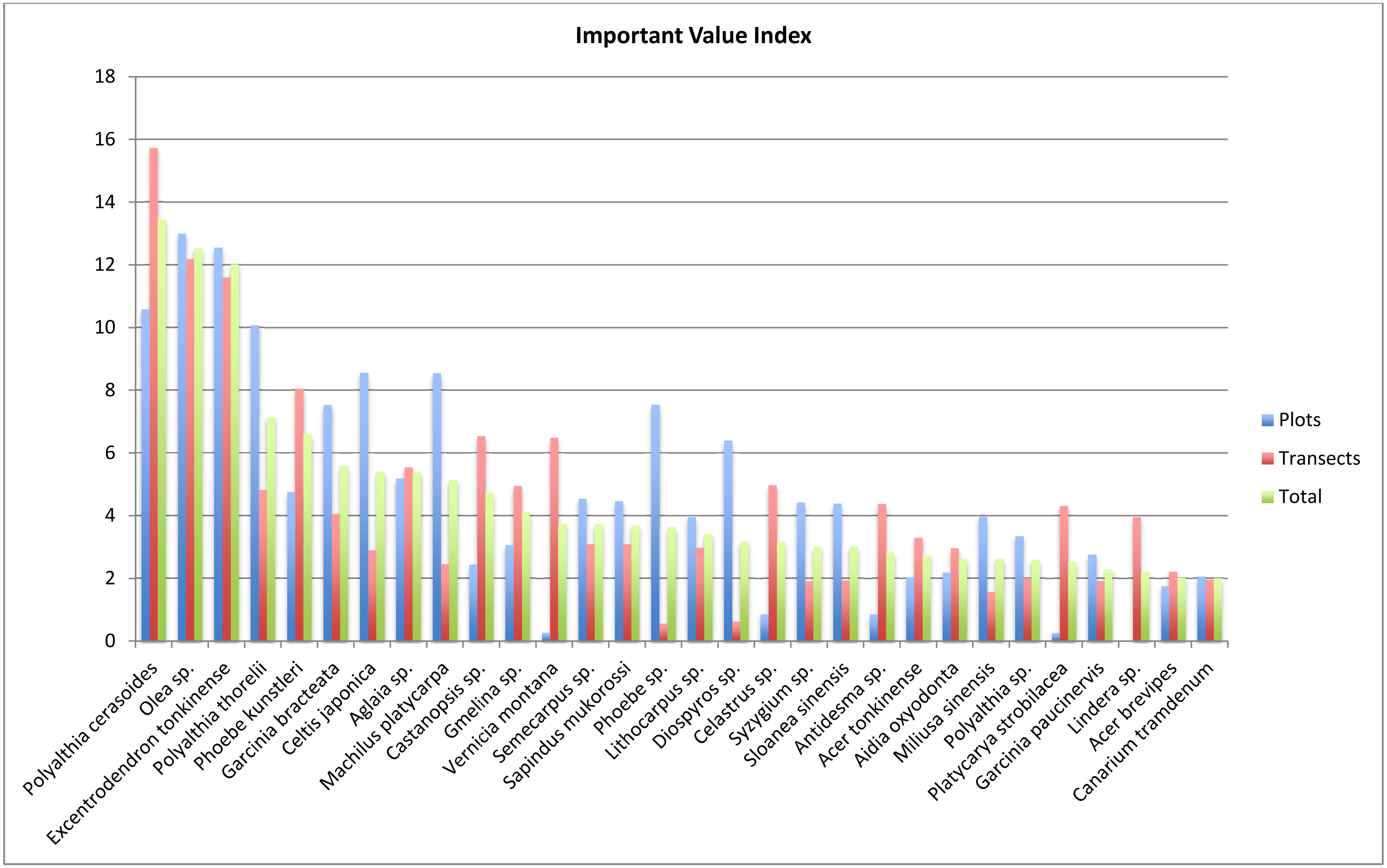

Figure 4.12. Percentage of Importance Value Index (IVI) for dominant plant species (IVI ≥ 2.0) by transects and plots

Forest Profile

The descriptions and illustration of Khau Ca forest structure are presented in Tables 4.7–11, and Figures 4.13–17.

Table 4.7. List of the plant species and families on Section A1200-1250 in Transect A

Tree ID	Family	Species	DBH (cm)	BA (cm^2)	Tree height (m)
A0069	Oleaceae	*Olea* sp.	16.9	224.32	12.0
A0070	Elaeocarpaceae	*Elaeocarpus griffithii*	12.7	126.68	10.0
A0071	Meliaceae	*Aglaia* sp.	14.0	153.94	10.0
A0072	Aquifoliaceae	*Ilex* sp.	37.5	621.70	12.0
A0073	Tiliaceae	*Excentrodendron tonkinense*	77.2	4,680.85	22.0
A0074	Oleaceae	*Olea* sp.	13.4	141.03	10.0
A0075	Lauraceae	*Phoebe kunstleri*	34.8	951.15	20.0
A0076	Annonaceae	*Polyalthia cerasoides*	13.3	138.93	7.0
A0077	Lauraceae	*Phoebe kunstleri*	23.7	441.15	22.0
A0078	Annonaceae	*Polyalthia cerasoides*	10.7	89.92	10.0
A0079	Styracaceae	*Styrax tonkinensis*	13.6	145.27	12.0
A0080	Oleaceae	*Olea* sp.	17.8	248.85	13.0
A0081	Tiliaceae	*Excentrodendron tonkinense*	114.2	10,242.88	20.0
A0082	Sapotaceae	*Sinosideroxylon wightianum*	24.7	479.16	26.0
A0083	Oleaceae	*Olea* sp.	17.2	232.35	12.0
A0084	Lauraceae	*Phoebe kunstleri*	55.4	2,410.51	18.0
A0085	Aquifoliaceae	*Ilex* sp.	11.0	95.03	10.0
A0086	Oleaceae	*Olea* sp.	30.8	745.06	12.0

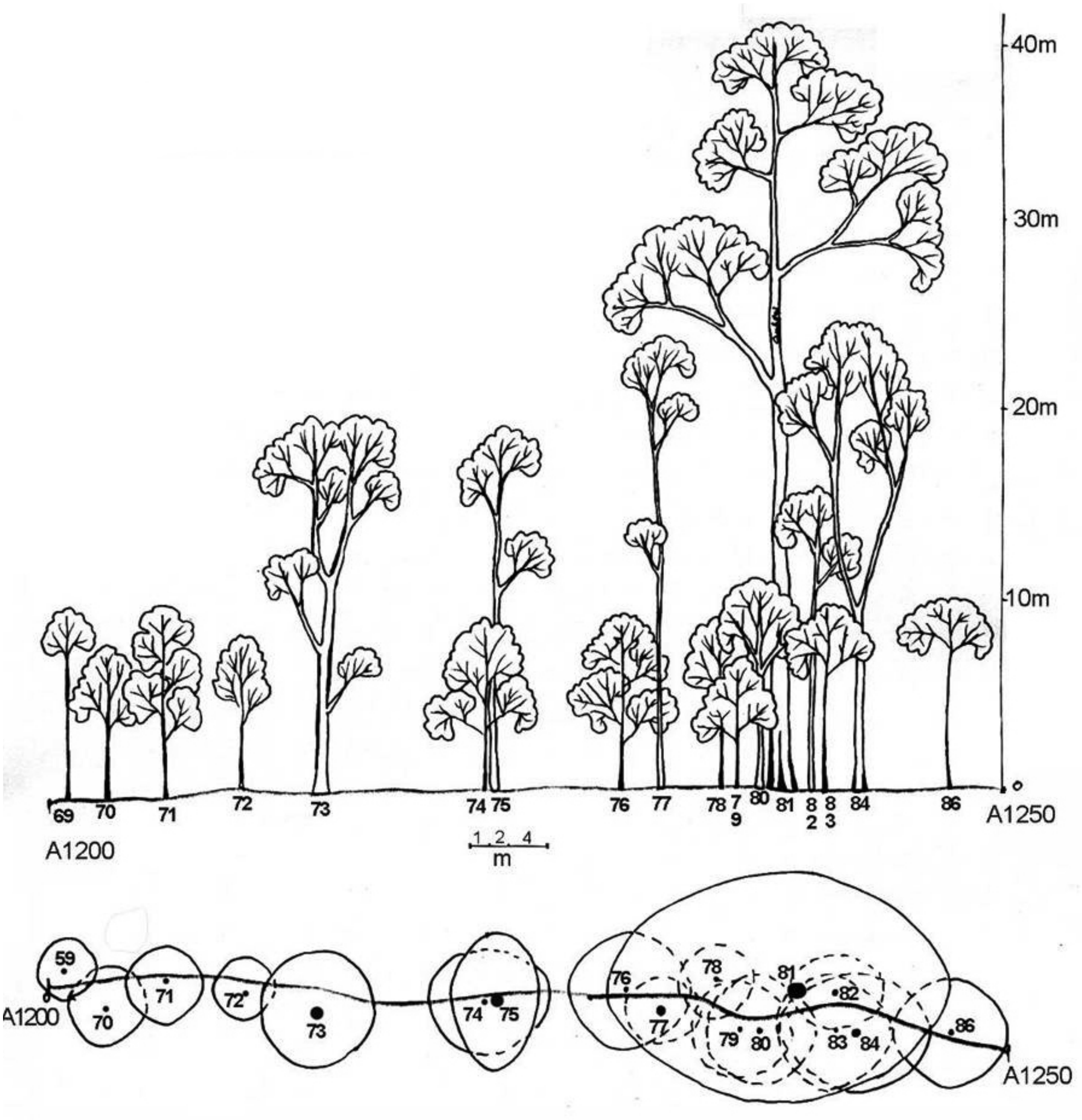

Figure 4.13. Profile diagram of Section A1200-1250 in Transect A
Note. Drawing by Mr. Vu Anh Tai

Table 4.8. List of the plant species and families on Section H1700-1750 in Transect A

Tree ID	**Family**	**Species**	**DBH** (cm)	**BA** (cm^2)	**Tree height** (m)
H0062	Ulmaceae	*Celtis tetrandra*	21.6	366.44	12.0
H0063	Aceraceae	*Acer tonkinense*	48.2	1,824.67	15.0
H0064	Annonaceae	*Polyalthia cerasoides*	40.1	636.84	10.0
H0065	Myrtaceae	*Decaspermum* sp.	28.1	620.16	14.0
H0066	Magnoliaceae	*Michelia* sp.	10.9	93.31	9.0
H0067	Clusiaceae	*Garcinia fagraeoides*	59.3	2,761.84	20.0
H0068	Annonaceae	*Polyalthia cerasoides*	29.3	359.22	10.0
H0069	Lauraceae	*Beilschmiedia* sp.	24.9	486.95	5.0
H0070	Annonaceae	*Polyalthia cerasoides*	38.9	607.91	12.0
H0071	Annonaceae	*Polyalthia cerasoides*	18.4	265.90	10.0
H0072	Myrtaceae	*Decaspermum* sp.	34.3	924.01	25.0
H0073	Oleaceae	*Olea* sp.	12.3	118.82	10.0
H0074	Aceraceae	*Acer tonkinense*	43.7	1,499.87	20.0
H0075	Clusiaceae	*Garcinia paucinervis*	13.2	136.85	7.0
H0076	Annonaceae	*Polyalthia cerasoides*	32.8	844.96	17.0
H0077	Clusiaceae	*Garcinia bracteata*	11.0	95.03	9.0
H0078	Burseraceae	*Canarium tramdenum*	30.0	706.86	18.0
H0079	Clusiaceae	*Garcinia bracteata*	10.5	86.59	8.0
H0080	Clusiaceae	*Garcinia fagraeoides*	10.1	80.12	8.0

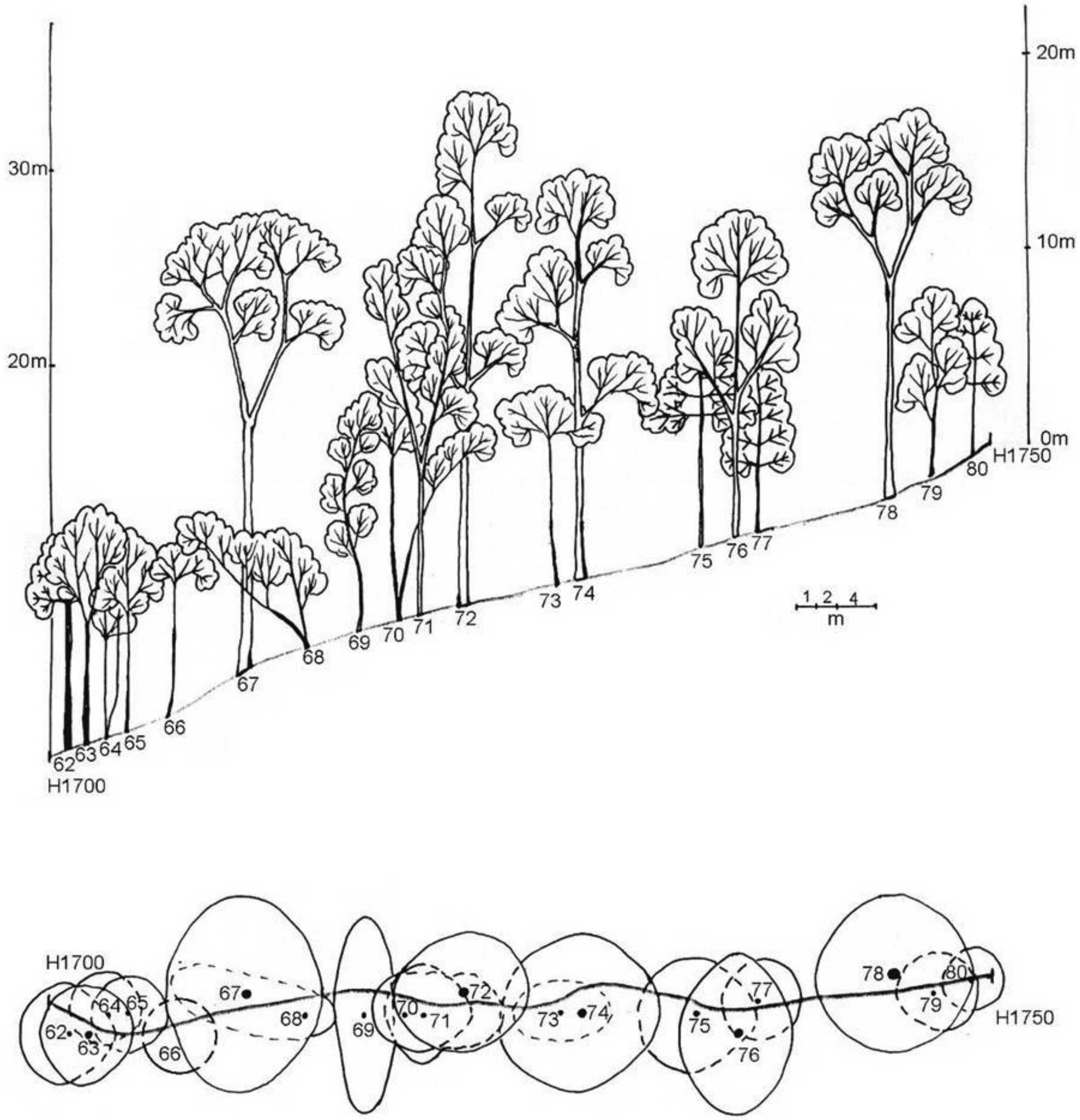

Figure 4.14. Profile diagram of Section H1700-1750 in Transect A
Note. Drawing by Mr. Vu Anh Tai

Table 4.9. List of the plant species and families on Section B1550-1600 in Transect B

Tree ID	**Family**	**Species**	**DBH** (cm)	**BA** (cm^2)	**Tree height** (m)
B0075	Clusiaceae	*Garcinia bracteata*	10.0	78.54	10.0
B0076	Juglandaceae	*Platycarya strobilacea*	47.0	1,734.94	17.0
B0077	Clusiaceae	*Calophyllum* sp.	22.8	408.28	15.0
B0078	Fagaceae	*Castanopsis* sp.	22.3	390.57	10.0
B0079	Fagaceae	*Castanopsis* sp.	15.8	196.07	8.5
B0080	Fagaceae	*Castanopsis* sp.	15.9	198.56	10.0
B0081	Clusiaceae	*Garcinia fagraeoides*	11.4	102.07	10.0
B0082	Fagaceae	*Castanopsis* sp.	16.1	203.58	12.0
B0083	Fagaceae	*Castanopsis* sp.	57.5	2,596.72	10.0
B0084	Illiciaceae	*Illicium parvifolium*	12.0	113.10	10.0
B0085	Clusiaceae	*Garcinia fagraeoides*	14.0	153.94	11.0
B0086	Illiciaceae	*Illicium parvifolium*	10.7	89.92	10.0
B0087	Aceraceae	*Acer brevipes*	13.7	147.41	8.0
B0088	Illiciaceae	*Illicium parvifolium*	9.6	72.38	9.0
B0089	Clusiaceae	*Garcinia fagraeoides*	16.0	201.06	10.0
B0090	Styracaceae	*Beilschmiedia* sp.	11.0	95.03	10.0
B0091	Aceraceae	*Acer brevipes*	28.4	633.47	12.0
B0092	Clusiaceae	*Garcinia fagraeoides*	13.5	143.14	15.0
B0093	Illiciaceae	*Illicium parvifolium*	15.5	188.69	10.0
B0094	Meliaceae	*Rhododendron* sp.	17.3	235.06	10.0
B0095	Clusiaceae	*Garcinia fagraeoides*	14.0	153.94	12.0
B0096	Fagaceae	*Castanopsis* sp.	13.5	143.14	12.0
B0097	Sapotaceae	*Sinosideroxylon wightianum*	29.9	702.15	13.0
B0098	Clusiaceae	*Garcinia fagraeoides*	14.3	160.61	9.0
B0099	Aceraceae	*Acer fabri*	14.5	165.13	8.0
B0100	Lauraceae	*Lindera* sp.	11.7	107.51	12.0

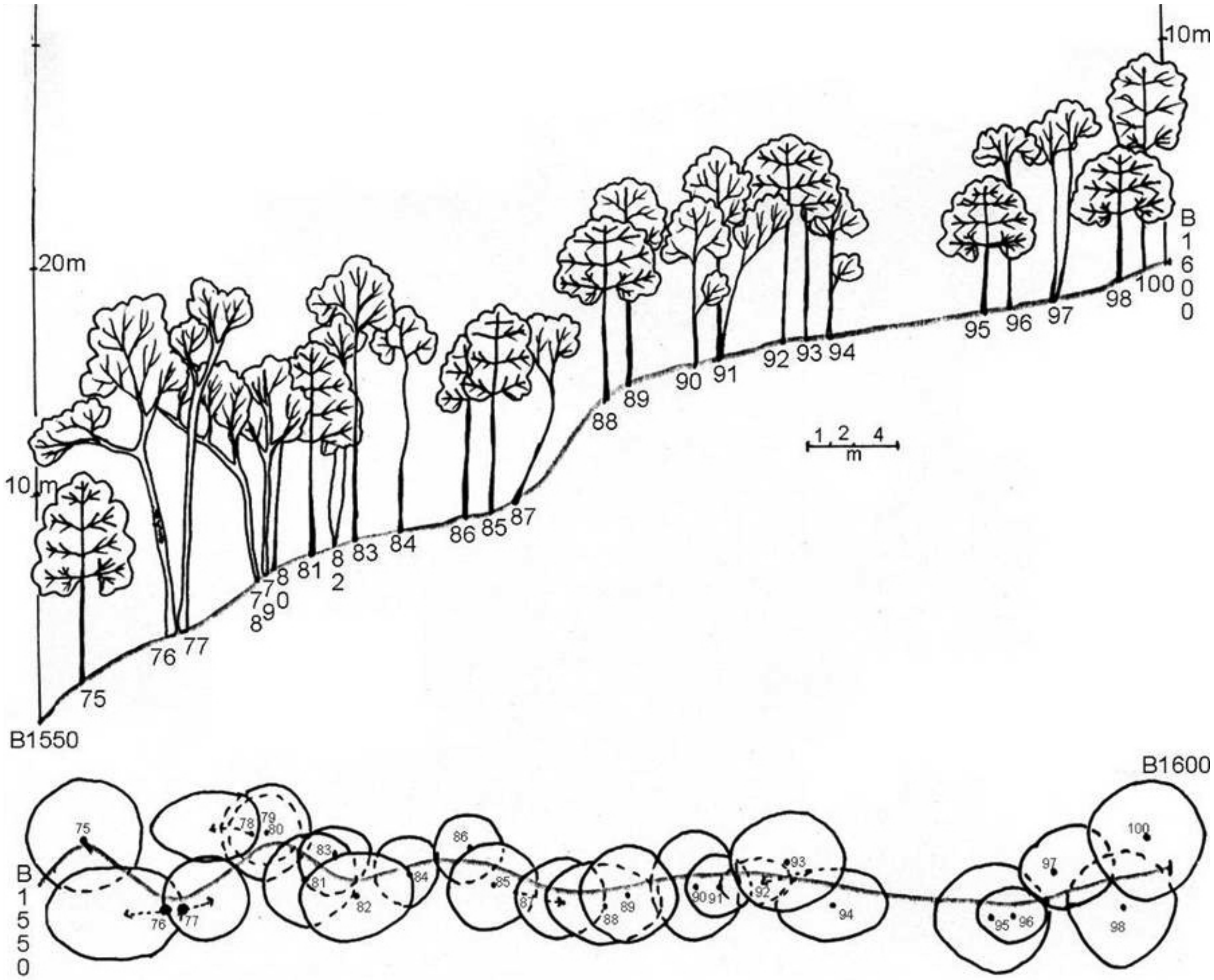

Figure 4.15. Profile diagram of Section B1550-1600 in Transect B
Note. Drawing by Mr. Vu Anh Tai

Table 4.10. List of the plant species and families on Section C1850-1900 in Transect C

Tree ID	**Family**	**Species**	**DBH** (cm)	**BA** (cm^2)	**Tree height** (m)
C0063	Oleaceae	*Olea* sp.	11.2	98.52	8.0
C0064	Sapindaceae	*Sapindus* sp.	37.9	1,128.15	20.0
C0065	Annonaceae	*Polyalthia thorelii*	22.0	380.13	16.0
C0066	Ulmaceae	*Celtis tetrandra*	42.6	1,425.31	20.0
C0067	Tiliaceae	*Excentrodendron tonkinense*	90.0	6,361.73	32.0
C0068	Oleaceae	*Olea* sp.	18.3	263.02	11.0
C0069	Rhamnaceae	*Ziziphus oenoplia*	50.7	2,018.86	20.0

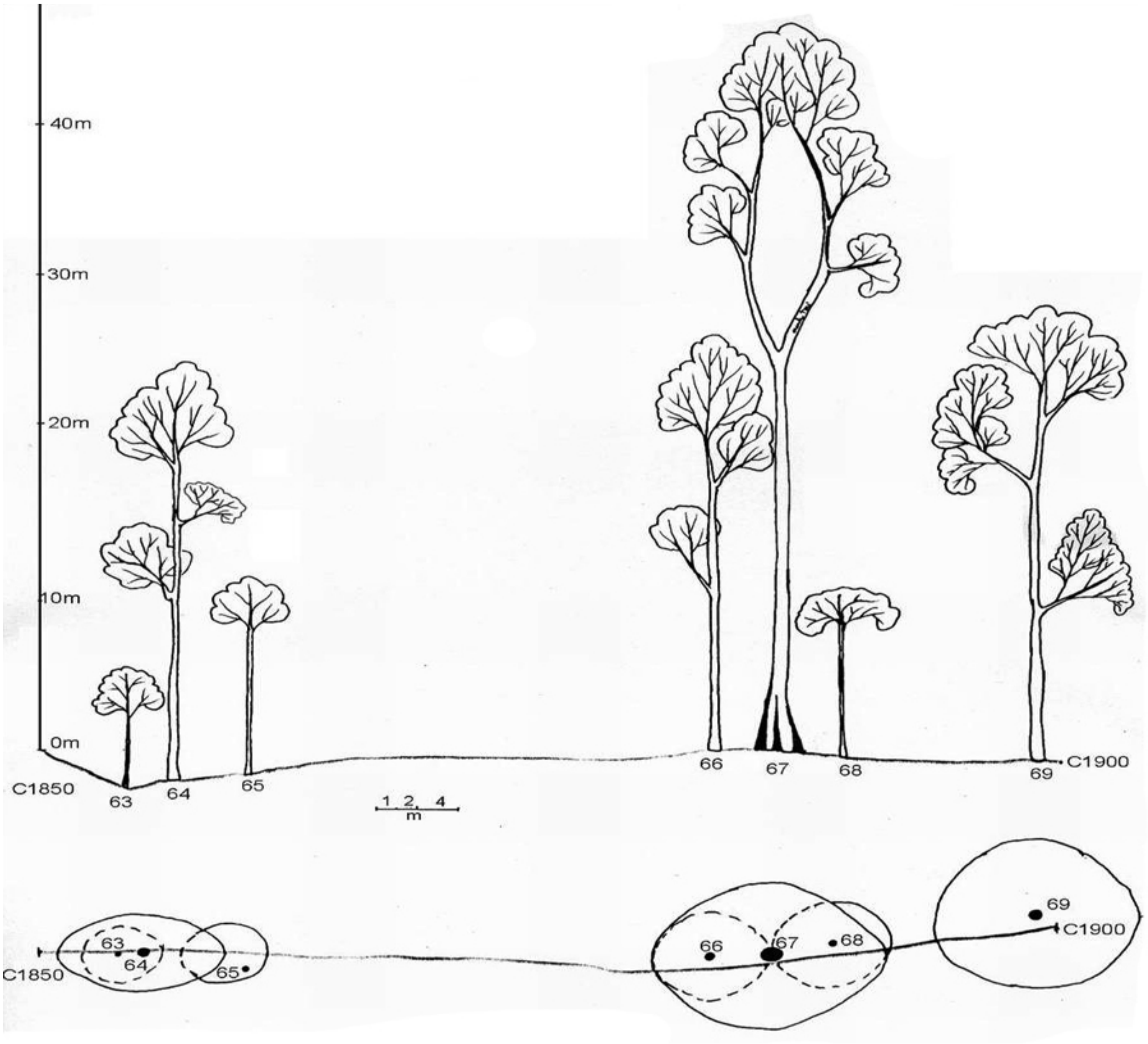

Figure 4.16. Profile diagram of Section C1850-1900 in Transect C
Note. Drawing by Mr. Vu Anh Tai

Table 4.11. List of the plant species and families on Section D850-900 in Transect D

Tree ID	**Family**	**Species**	**DBH** (cm)	**BA** (cm^2)	**Tree height** (m)
D0063	Clusiaceae	*Calophyllum* sp.	54.3	2,315.74	20.0
D0064	Tiliaceae	*Excentrodendron tonkinense*	12.4	120.76	12.0
D0066	Rubiaceae	*Aidia cochinchinensis*	10.6	88.25	8.0
D0067	Annonaceae	*Polyalthia cerasoides*	102.0	2,066.15	10.0
D0068	Annonaceae	*Polyalthia cerasoides*	24.7	479.16	8.0
D0069	Flacourtiaceae	*Hydnocarpus kurzii*	24.8	483.05	10.0
D0070	Euphorbiaceae	*Antidesma* sp.	12.4	120.76	7.0
D0071	Bignoniaceae	*Radermachera sinica*	37.1	1,081.03	14.0
D0072	Annonaceae	*Polyalthia cerasoides*	14.4	162.86	10.0
D0073	Annonaceae	*Polyalthia cerasoides*	21.4	359.68	12.0
D0075	Annonaceae	*Polyalthia cerasoides*	88.0	1,654.00	10.0
D0076	Euphorbiaceae	*Triadica sebiferum*	52.4	2,156.51	17.0
D0077	Sapindaceae	*Sapindus saponaria*	48.9	1,878.05	15.0

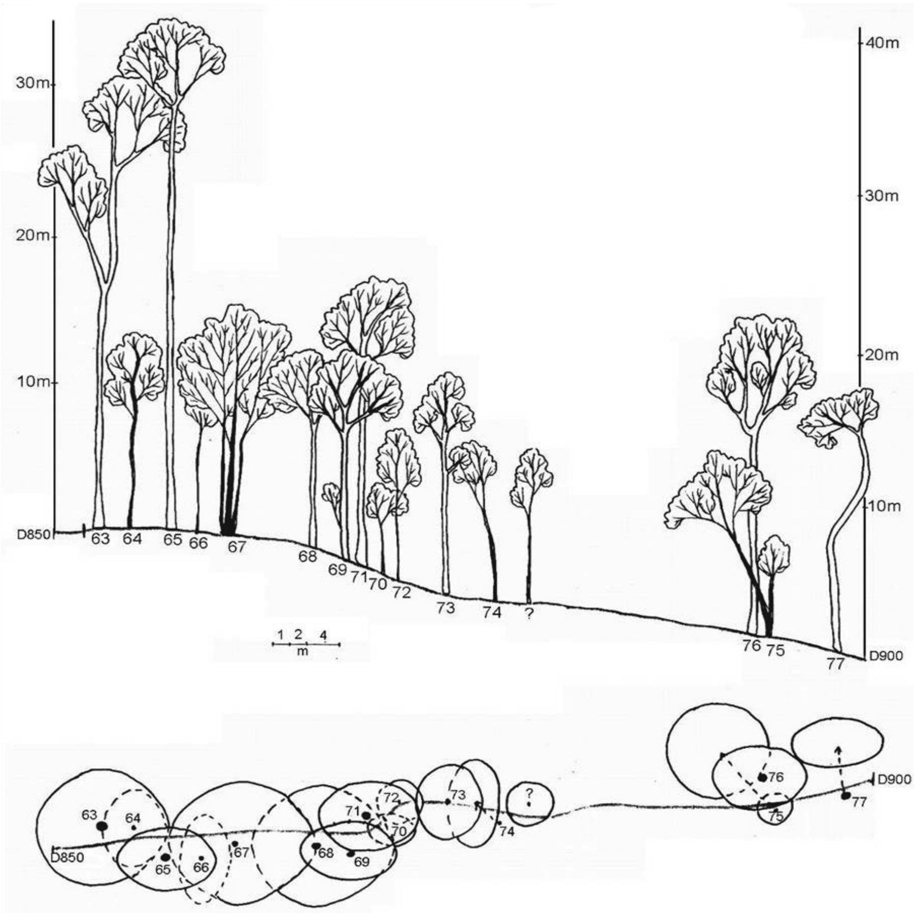

Figure 4.17. Profile diagram of Section D850-900 in Transect D
Note. Drawing by Mr. Vu Anh Tai

4.4. Discussion

4.4.1. Forest Structure

Tree density of Khau Ca Forest is relatively similar to other study sites in Vietnam, Lao PDR, Cambodia and China (Table 4.12). This study documented that there are 513 stems/ha in the Khau Ca Forest. In Na Hang Nature Reserve, Dong Thanh Hai (2011) estimated 956 stems/ha, however, he used a smaller measurement of trees at DBH at 6 cm or greater, while the current study uses 10cm or greater. In the Samage Forest, Grueter (2009) reported on the habitat of the black snub-nosed monkeys (*Rhinopithecus bieti*) and found densities of 518 – 950 stems/ha depending on various forest types. Ulibarri (2013) and Phiapalath (2009) estimated 441 – 708 stems/ha and 427 stems/ha in the Son Tra Nature Reserve, Vietnam and Hin Namno National Protected Area, Lao PDR respectively; areas that are home to the red-shanked doucs (*Pygathrix nemaeus*). Ha Thang Long (2009) estimated 615 stems/ha in the Kon Ka Kinh National Park inhabited by the grey-shanked doucs (*Pygathrix cinerea*). In contrast, tree density in habitats of the black-shanked doucs (*Pygathrix nigripes*) is lower: Hoang Minh Duc (2007) reported 206 – 467 stems/ha for Nui Chua National Park, and 111.4 – 388.3 stems/ha for Phuoc Binh National Park, Blanc *et al*. (2000) documented 195 – 540 stems/ha for Cat Tien National Park, and Rawson (2009) estimated 350 – 507 stems/ha for Seima Biodiversity Conservation Area.

Total basal area of the Khau Ca Forest is also relatively similar to other study sites in Vietnam, Lao PDR, Cambodia, and China. Total basal area in Khau Ca Forest is 45.6 m^2/ha, smaller than Na Hang Nature Reserve, 58.95 m^2/ha (Dong Thanh Hai, 2011) and Kon Ka Kinh National Park, 50.70 – 52.38 m^2/ha (Ha Thang Long, 2009); similar to parts of Son Tra Nature Reserve, 43.10 – 56.90 m^2/ha (Ulibarri, 2013) and Hin Namno National Protected Area, 29.30 – 69.41 m^2/ha; and relatively greater than Seima Biodiversity Conservation Area, 28.98 – 33.47 m^2/ha (Rawson, 2009).

Table 4.12. Summary of forest structure data from other studies compared to this study

Species	Location	Min. DBH (cm)	No. Measured Stems (n)	BA (m$^{2/}$ha)	Tree density (stems/ha)
Rhinopithecus avunculus	Khau Ca SHCA, Vietnam[1]	10	2,772	45.60	513
	Na Hang NR, Vietnam[2]	6	612	58.95	956
Rhinopithecus bieti	Samage Forest, China[3]	12.7			
	Mixed deciduous broadleaf/conifer forest		966	–	697.8 (248.1)
	Pine forest		325	–	812.5 ± 239.0
	Evergreen broadleaf forest		249	–	518.8± 146.6
	Cool temperate fir forest		241	–	860.7 ± 190.3
	Montane sclerophyllous oak forest		114	–	950.0 ± 413.1
Pygathrix nemaeus	Son Tra, Vietnam[4]	10	512	43.10 – 56.90	441 – 708
	Hin Namno NPA, Lao PDR[5]	10	640	29.30 – 69.41	427
Pygathrix nigripes	Nui Chua NP, Vietnam[6]	10	–	–	335.4 ± 64.2 (206 – 467)
	Phuoc Binh NP, Vietnam[6]	10	–	–	293.9 ± 72.1 (111.4 – 388.3)
	Cat Tien NP, Vietnam[7]	10	2,012	29.30 – 69.41	195 – 540
	Seima BCA, Cambodia[8]	10	545	28.98 – 33.47	350 – 507
Pygathrix cinerea	Kon Ka Kinh NP, Vietnam[9]	10		50.70 – 52.38	615

Note. SHCA: Species/Habitat Conservation Area, NR: Nature Reserve, NP: National Park, NPA: National Protected Area, BCA: Biodiversity Conservation Area. [1] This study, [2] Dong Thanh Hai (2011), [3] Grueter *et al.* (2013), [4] Ulibarri (2013), [5] Phiapalath (2009), [6] Hoang Minh Duc (2007), [7] Blanc *et al.* (2000), [8] Rawson (2009), [9] Ha Thang Long (2009).

At the family level, in term of stem number, Annonaceae (n = 373; 13.46%) was the most dominant in the Khau Ca Forest with total basal area of 24.13 m^2 (4.47 m^2/ha 9.80%). However, in terms of total basal area, Tiliaceae was the most dominant with total basal area of 30.11 m^2 (5.58 m^2/ha; 26.98%) in term of total basal area. The ten most dominant families comprised 77.50% of total basal area in the Khau Ca Forest. Among of top ten families Dong Thanh Hai (2011) recorded in Tat Ke Sector of Na Hang Nature Reserve, there were four families including Annonaceae, Lauraceae, Euphorbiaceae and Clusiaceae that were also among most abundant families in Khau Ca. In Na Hang, Tiliaceae was the most dominant in term of total basal area (Dong Thanh Hai, 2011). In both areas of Tat Ke and Khau Ca, *Excentrodendron tonkinensis* (Tiliaceae) was the most common large trees.

Le Khac Quyet *et al.* (2007) found 31 plant species belonging to 21 families were consumed by *R. avunculus* in Khau Ca Forest. The plant species most frequently consumed with *Iodes seguini* (Icacinaceae) (young leaves, petioles and ripe fruits), *Garcinia* spp. (Clusiaceae) (petioles, fruits), *Acer tonkinense* (Aceraceae) (leaf stems), *Excentrodendron tonkinensis* (young leaves, flowers and unripe fruits) and *Brassaiopsis* spp. (Araliaceae) (ripe fruits) being most frequently consumed (Le Khac Quyet *et al.*, 2007). When analyzing selected foods by family, *R. avunculus* appear to be quite liberal in their selection of food items. Of the 57 tree families captured by the six transects and 30 plots, 17 (29.82%) were in the diet of *R. avunculus*. The total number of trees in the transects and plots of the families that *R. avunculus* consumed was 1,323 (47.73%) with total basal area of 153.97 m^2 (62.52%). However, the analysis by genus suggests greater discrimination. Of the 123 identified tree genera, 16 (13.01%) were eaten by *R. avunculus*. This represents 768 (27.71%) out of a total of 2,772 trees identified to genus. Thus, *R. avunculus* appear to be quite selective in diet when more exclusive taxonomic categories are analyzed.

4.4.2. Phenology

The Khau Ca Forest is located within the “Northern Indochina Subtropical Moist Forests Ecoregion of the Indo-Pacific Region” (Averyanov *et al.*, 2003; Wikramanayake *et al.*, 2002) and belongs to the South Chinese floristic province of the Indochinese floristic region of the Indomalesian sub-kingdom of the Paleotropic Realm. According to Nguyen Khanh Van *et al.* (2000), the climate of the Khau Ca Forest is tropical monsoon with cold and dry winters from October to March, and hot and rainy summers from April to September. Therefore, the effects of seasonal climate clearly affected plant productivity patterns in Khau Ca.

As can be seen from Figures 4.9-11, there were more new (young) leaves available from March to June with two peaks of leafing production in April and June with 45.30% and 48.57% of all trees respectively having new leaves. In contrast, there are more fruits available in the rainy months from June to September. A peak in flower availability occurred from March to May. The productivity of new leaves and fruits show a significant positive correlation to temperature and rainfall respectively. Similar results were also found in Tat Ke Sector of Na Hang Nature Reserve (Dong Thanh Hai, 2011).

4.3.4. Habitat Capacity

Based on my observations and monitoring data in 2009 – 2010, I estimated that there are about 92 – 100 *R. avunculus* individuals in the Khau Ca Forest. Dong Thanh Hai (2011) provided a similar estimate of 81 – 90 individuals in 2006, as did Le Van Dung (2013) with an estimate of 73 – 90 in 2013. Based on the quality of forest coverage it is estimated that about 7.00 km^2 of the Khau Ca Forest is suitable habitat for *R. avunculus*. This area is referred to as the core zone of the Khau Ca Forest, so *R. avunculus* population density based on my population estimate is about 13.1 – 14.2 individuals/km^2. Khau Ca’s *R. avunculus* population density is higher than in Tat Ke Sector of Na Hang Nature Reserve that was estimated at 8 individuals/km^2 (Boonratana and Le Xuan Canh, 1998) although presumably it is much lower today (see Thach Mai Hoang, 2011). Khau Ca population density is also higher than population densities of the Chinese snub-nosed monkeys: 8 individuals/km^2 of golden snub-nosed monkey (*R. roxellana*) in

Shenongjia National Nature Reserve (Ren *et al.*, 1998), 7 individuals/km2 of black and white snub-nosed monkey (*R. bieti*) in Wuyapiya Area (Kirkpatrick *et al.*, 1998), and 11 individuals/km^2 of gray snub-nosed monkey (*R. brelichi*) in Fanjingshan National Nature Reserve (Bleisch *et al.*, 1993). Snub-nosed monkey population densities are relatively lower than some other odd-nosed monkeys, e.g., 34 – 63 individuals/km^2 of proboscis monkey (*Nasalis larvatus*) in peat swamps of Malaysia (Boonratana, 2000; Yeager, 1989, 1990), 21 – 220 individuals/km^2 of simabokou (*Simias concolor*) in peat swamp of Pagai Island and dipterocarp forest of Grukna, Indonesia (Tenaza and Fuentes, 1995; Watanabe, 1981). Some of the reported densities for doucs are quite low; 5.8 ± 4.7 group/km^2 of red-shanked douc (*Pygathrix nemaeus*) in Hin Namno National Protected Area, Lao PDR (Phiapalath, 2009); 4.3 individuals/km^2 of red-shanked douc (*Pygathrix nemaeus*) in Son Tra Nature Reserve, Vietnam (Lippold and Vu Ngoc Thanh, 2008) and 0.6 individuals/km2 of grey-shanked douc (*P. cinerea*) in the Kon Ka Kinh National Park (Ha Thang Long, 2009). Population densities of snub-nosed monkeys and other odd-nosed monkeys depend on their habitat qualities and resources. For instances, the Chinese snub-nosed monkeys live in temperate to alpine forests which might account for a lower population density (see Kirkpatrick, 2011). However, the lower densities of *P. nemaeus* at Son Tra Nature Reserve (Lippold and Vu Ngoc Thanh, 2008) and *P. cinerea* at Kon Ka Kinh National Park (Ha Thang Long, 2009) are not easily explained by habitat qualities and/or resources because hunting is likely a factor impacting their densities.

Summary

- Six 1,000-by-2-meter transects and thirty 20-by-50-meter plots were established in the home range of *Rhinopithecus avunculus* in the Khau Ca Forest. All trees with DBH at 10 cm or greater were measured and identified for forest structure analysis.
- The physical structure of forest was characterized by tree density of 513 stems/ha, mean tree height of 14 ± 6.8 m, mean DBH of 27.7 ± 23.0 cm, total basal area of 45.60 m^2/ha, and mortality rate of 13 stems/ha/year.

- Flowering patterns differed across the six transects. Peak production occurred in March through May in 2010. Productivity of flowers was not significantly correlated to rainfall and temperature.
- Fruiting patterns also differed across the six transects. Peak production occurred in June through September in 2010. Productivity of fruit was not significantly correlated to rainfall and temperature.
- Leafing patterns also differed across the six transects. Peak production occurred in April through August in 2010. Productivity of young leaves was significantly correlated to temperature and rainfall.
- Within the six transects and 30 plots, there was a total 2,772 trees belonging to 109 identified species and 73 unidentified species belonging to 123 genera and 57 families. Species diversity index (Shannon-Wiener H' Index) was 4.33. Annonaceae had the highest density (13.46%) and Tiliaceae had the largest basal area (26.98%). *Olea* sp. (Oleaceae) was the commonest tree in the Khau Ca Forest.
- *R. avunculus*' food resources in Khau Ca are sufficient to maintain a large *R. avunculus* population.

CHAPTER V

POSITIONAL REPERTOIRE AND SUPPORT USE

5.1. Introduction

The aims of this chapter are to describe the overall positional repertoire (patterns of locomotion and postures) and to further examine the relationship between positional behavior (with associated maintenance activities such as travel and foraging) and support use (number, size, orientation and flexibility) of adult male *R. avunculus* in the Khau Ca Forest, Ha Giang Province, Vietnam.

Because there are no studies to compare to and to develop hypotheses of positional behavior for *R. avunculus* (e.g., Boonratana and Le Xuan Canh, 1998; Covert *et al.*, 2008) and there are relatively few studies of other members of the genus *Rhinopithecus* (e.g., Grueter *et al.*, 2013; Isler and Gruter, 2006; Kirkpatrick *et al.*, 1999; Kirkpatrick and Long, 1994; Li, 2007). Rather, hypotheses and predictions are based on broad ideas about positional behavior for primates in general, and more specific ideas about colobine positional behavior drawn from the primary literature and on more than 500 hours of qualitative observations on *R. avunculus* at Khau Ca since January 2002. Important literature that was carefully reviewed includes Bitty and McGraw (2007), Byron and Covert (2004), Cannon and Leighton (1994), Cant (1987, 1988, 1992), Doran (1993), Fleagle (1976, 1977), Fleagle and Mittermeier (1980), Gebo and Chapman (1995a, 1995b), McGraw (1996a, 1998a, 1998b, 2000), Mittermeier and Fleagle (1976), Morbeck (1977), Stevens *et al.* (2008), Workman and Covert (2005), and Wright *et al.* (2008).

The hypotheses concerning positional behavior and support use addressed by this study are as follows:

Hypothesis 5.1: Given that *R. avunculus* is a large-bodied arboreal colobine, its locomotor repertoire will include higher frequencies of leaping (*sensu* McGraw, 1998a), suspensory behaviors and climbing, and lower frequencies of running and walking; and its postural repertoire will include higher frequencies of sitting, lying and quadrupedal standing, and lower frequencies of bipedal stand and cling compared to other smaller-bodied colobines.

This hypothesis is based on results of association between body size and positional behavior among primates by Crompton (1983), Crompton (1984), Fleagle and Mittermeier (1980), Gebo and Chapman (1995b), McGraw (1998a, 1998b), and Rose (1979). According to Fleagle and Mittermeier (1980), in a given arboreal habitat, larger-bodied animals leap less, climb more frequently, and bridge more often than smaller-bodied animals, and engage in relatively more frequent suspensory behavior. Crompton (1983) tested Fleagle and Mittermeier's (1980) findings in a study of two galago species, and his results corroborated the findings of decreased leaping and increased climbing with increasing body size. However, studies by Gebo and Chapman (1995b), and McGraw (1998a, 1998b) found correlation between body size and positional behavior among Old World monkeys to differ from the findings of Fleagle and Mittermeier (1980). Specifically, Gebo and Chapman (1995b) found that there were no clear intra- and interspecific differences in locomotor behavior and substrate use by five studied species of *Cercopithecus* and *Colobus* in Kibale Forest. Among Tai Forest monkeys, McGraw (1998a, 1998b) found that body size was not a consistent predictor of leaping frequency; larger-bodied colobines tended to leap more that smaller-bodied cercopithecines. Among colobines, the smallest species leaped the most and vice versa among cercopithecines whereas colobines sit more and stand less than cercopithecines. Based on studies by Rawson (2009), Workman and Schmitt (2012), Zhou *et al.* (2013), and Xiong *et al.* (2009) it has been assumed that among of Asian colobines, larger-bodied animals more frequently use quadrupedalism and climb, and less frequently leap and sitting is most frequently during resting and feeding.

Hypothesis 5.2: Given its large-bodied size *R. avunculus* will more frequently use large- and medium-sized supports in their locomotor and postural behaviors compared to other smaller-bodied colobines.

This hypothesis is based on suggestion of Fleagle and Mittermeier (1980) that "larger monkeys should use larger supports in order to sustain their greater weight, [and] ...to maintain their center of gravity above the branch" (p. 310). Gebo and Chapman (1995b) found all five cercopithecids in Kibale Forest, Uganda prefered medium-sized supports (i.e., branches) and the larger-bodied species used larger supports more often than did smaller-bodied species. McGraw (1998a,b) reported the same trend of support use for five cercopithecids in Tai Forest, Ivory Coast. Studies of Fleagle (1978), Rawson (2009), and Grueter *et al.* (2013) also showed that Asian colobines used medium-sized supports most frequently.

The questions addressed in this chapter are:

- What are the defining and unique characteristics of *R. avunculus*' positional behavior?
- How do *R. avunculus* utilize the available substrates within their habitat at Khau Ca?

5.2. Methods

This section only outlines statistical methodologies utilized for analysis of positional behavior and support use of *R. avunculus* in this chapter. See Chapter III for general details about protocols for animal habituation, behavioral data collection, and sampling methods used in this study.

I collected frequency data on the positional behavior of *R. avunculus* using a bout sampling technique on a focal animal following Fleagle (1976). To avoid any confounding affects that age- and sex-based differences may have on these data, only data on adult males are presented in this chapter; sex-based and age-based differences in positional behavior and support use of *R. avunculus* are examined in Chapters VI and VII.

I used an extensive list of possible locomotor and postural categories taken from Hunt *et al.* (1996) (see Chapter III, Table 3.2). This list was developed prior to this study using other positional behavior studies on comparable species as reference and adjusted based on early observations made while following *R. avunculus* in Khau Ca Forest. These locomotion and postures of adult, juvenile and infant *R. avunculus* are listed in Table 5.1.

Following Bitty and McGraw (2007), Doran (1993), McGraw (1996a, 1998b, 2000), and Youlatos (1998a, 1999, 2002) I used G-tests for independence using Bonferroni correction (MacDonald, 2008) to compare frequency tables generated for each group's overall positional profile and each group's locomotor and postural profiles by associated maintenance activity. Significant results for all tests ($p \leq 0.05$) indicate a dependent relationship between column and row variables. All tests were two-tailed and performed using applications of Microsoft Excel and JUMP Pro 11 for Mac.

During analysis, similar positional behaviors were grouped into broad categories (Table 5.2). Grouped categories produced fewer columns on frequency tables and were necessary in order to avoid generating frequency tables in which more than 20% of entries had expected counts are less than 5 as minimal requirements for statistical tests (see MacDonald, 2008; McKillup, 2012; Sokal and Rohlf, 2009).

Table 5.1. Locomotor and postural behaviors observed for *R. avunculus* in Khau Ca Forest from February 2009 to December 2010

	IF	J1	J2	SAM	A
Locomotion					
Arm-swing	x	x	x	x	x
Bihop	x	x	x		x
Bipedal walk	x	x	x		x
Bridge		x	x		x
Drop					
Bimanual suspensory drop	x	x	x	x	x
Quadrupedal drop	x	x	x	x	x
Unimanual suspensory drop		x	x	x	x
Leap					
Pronograde leap	x	x	x	x	x
Pumping leap	x	x	x	x	x
Vertical cling leap		x	x	x	x
Quadrupedal run	x	x	x	x	x
Quadrupedal walk	x	x	x	x	x
Vertical climb					
Ladder climb		x	x	x	x
Pulse climb	x	x	x	x	x
Rump-first descent	x	x	x	x	x
Vertical scramble	x	x	x	x	x

Note. IF: Infant, J1: Juvenile 1, J2: Juvenile 2, SAM: Subadult male, A: Adult. Detailed description of age-sex categories of *R. avunculus* is in Table 3.1. Detailed descriptions of locomotor and postural behaviors (Hunt *et al.*, 1996) are in Table 3.2

Table 5.1 (continued)

	IF	J1	J2	SAM	A
Postures					
Bipedal stand					
Bipedal stand/forelimb suspend	x	x	x		x
Extended bipedal stand		x	x		x
Cling					
Bimanual cling	x	x	x	x	x
Unimanual cling	x	x	x		x
Forelimb-suspend					
Bimanual forelimb-suspend	x	x	x		x
Unimanual forelimb-suspend	x		x		x
Lie					
Lateral lie	x	x	x		x
Sit/lie		x	x		x
Sprawl		x	x	x	x
Supine lie	x	x	x		x
Sit					
Angled sit	x	x	x		x
Foot-prop sit			x	x	x
Ischium-sit			x		x
Sit-in	x	x	x	x	x
Sit-in/out	x	x	x	x	x
Sit-out	x	x	x	x	x
Sit/forelimb suspend	x	x	x	x	x
Stand					
Crouch	x	x	x	x	x
Quadrupedal stand	x	x	x	x	x

Note. IF: Infant, J1: Juvenile 1, J2: Juvenile 2, SAM: Subadult male, A: Adult. Detailed description of age-sex categories of *R. avunculus* is in Table 3.1. Detailed descriptions of locomotor and postural behaviors (Hunt *et al*., 1996) are in Table 3.2

Table 5.2. Grouped locomotor and postural categories

Lumped Category	Positional Behaviors Included
<u>Locomotion:</u>	
Quadrupedalism	- Quadrupedal walk
	- Quadrupedal run
Leap	- Pronograde leap
	- Pumping leap
	- Vertical cling leap
Climb (= Vertical climb)	- Ladder climb
	- Pulse climb
	- Rump-first descent
	- Vertical scramble
Drop	- Unimanual suspensory drop
	- Bimanual suspensory drop
	- Quadrupedal drop
Arm-swing	- Forelimb swing (= arm swing)
Other locomotion	- Bihop
	- Bridge
	- Bipedal walk
<u>Postures:</u>	
Sit	- Angled sit
	- Sit/forelimb suspend
	- Sit-in
	- Sit-out,
	- Sit-in/out
	- Ischium-sit
	- Foot-prop sit
Stand	- Quadrupedal stand
	- Crouch
Lie	- Lateral lie
	- Sit/lie
	- Sprawl
	- Supine lie
Cling	- Unimanual cling
	- Bimanual cling
Other posture	- Bipedal stand:
	o Bipedal stand/forlimb suspend
	o Extended bipedal stand
	- Forelimb suspend (= arm-hang):
	o Bimanual forelimb-suspend
	o Unimanual forelimb-suspend

5.3. Results

No terrestrial positional behavior of *R. avunculus* was recorded in this study, and this is consistent with my previous field observations, *R. avunculus* was rarely observed on the ground.

Tonkin snub-nosed monkeys exhibited a total of 9 locomotor modes (19 submodes) and 6 postural modes (16 submodes) (Table 5.1). Overall, there were significant differences in positional behaviors and maintenance activities ($G = 2618,423$, $p < 0.0001$), and positional behaviors and support use (Support number: $G = 108.267$, $p < 0.0001$; Support size: $G = 144.396$, $p < 0.0001$; Support orientation: $G = 722.361$, $p < 0.0001$; and Support flexibility: $G = 92.863$, $p <0.0001$). In general, the most frequent locomotor modes were quadrupedalism, leap, climb and drop; and the most frequent postural modes were sit, stand and lie.

5.3.1. Locomotion

Total sample size for adult male locomotion was 861 bouts. The most frequent locomotor activity is quadrupedalism accounting for 53.31% of all locomotor bouts, followed by leap (15.56%), climb (13.24%), drop (10.57%), arm-swing (5.23%) and other locomotor behaviors (bipedal hop, bridge, bipedal walk) (2.09%) (Table 5.3).

Proportions of different locomotor modes used during travel and foraging were divided by summing total bouts for the various categories and calculating percentages. When locomotion and associated maintenance activities are compared, there was not significant independence in locomotor behaviors and associated maintenance activities (travel and forage) employed by *R. avunculus* ($G = 7.808$, n.s.). Quadrupedalism dominated all activities during travel and foraging. Leap, climb and drop were used much more frequently during travel than during foraging. Arm-swing was used only during travel (Table 5.3, Figure 5.1).

Table 5.3. Locomotor profile of *R. avunculus* in Khau Ca Forest

	Forage		**Travel**		**Overall locomotion**		
	n	%	n	%	n	%	
Quadrupedalism	20	71.43%	439	52.70%	459	53.31%	n.s.
Leap	2	7.14%	132	15.85%	134	15.56%	n.s.
Climb	4	14.29%	110	13.21%	114	13.24%	n.s.
Drop	2	7.14%	89	10.68%	91	10.57%	n.s.
Arm-swing	-	-	45	5.40%	45	5.23%	n.s.
Other locomotion	-	-	18	2.16%	18	2.09%	n.s.
Total	*28*	*100.00%*	*833*	*100.00%*	*861*	*100.00%*	

Note. The last column represents significance of differences between frequencies of travel and forage after comparisons using Bonferroni correction. n.s.: not significant. Overall travel vs. forage: G = 7.808 n.s.

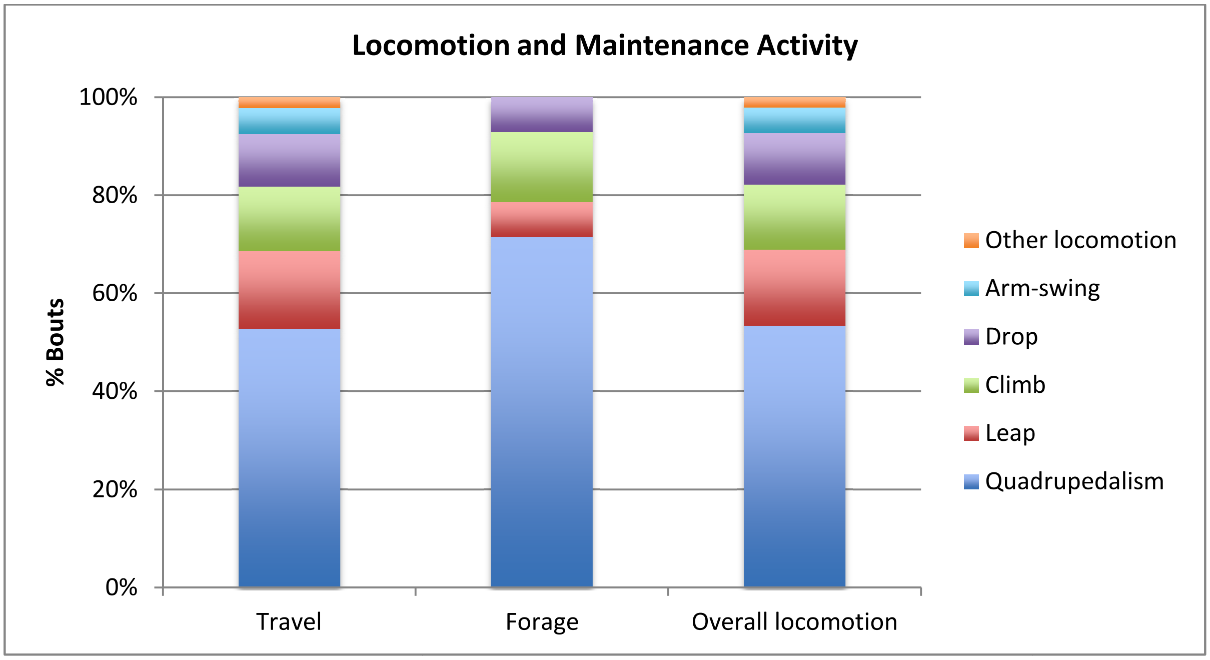

Figure 5.1. Frequencies of locomotor behaviors during travel, foraging and overall for *R. avunculus* in Khau Ca Forest

5.3.2. Locomotion and Support Use

There were significant differences in associated maintenance activities, locomotor behaviors and support use by *R. avunculus* (Tables 5.4–6).

Single and combined supports were most frequently used during travel and foraging by all locomotor modes (Tables 5.4–5; Figure 5.2). *R. avunculus* traveled most often on single supports (77.43%) and next on combined supports (16.93%) and less often on multiple and network supports (4.35 % and 1.63% respectively). During foraging, *R. avunculus* often used both single and combined supports, and used multiple and network supports more often than travel (Table 5.5).

Branches and boughs were most frequently used during travel and foraging by all locomotor modes. *R. avunculus* most commonly traveled on branches (73.83%) and boughs (17.89%), and most commonly foraged on branches (64.29%) and twigs (21.43%) (Table 5.4; Figure 5.2). Climbing was the most common locomotion of tree trunks. Lianas were used only for climbing (Tables 5.4–5; Figure 5.2).

Horizontal supports were most often used in both travel (45.38%) and foraging (39.29%) by all locomotor modes (45.18%). Oblique supports were the next most frequently used support by all locomotor types with the exception of climbing. Terminal and vertical supports were used more often in foraging than travel. Vertical supports were most frequently used by climb (Tables 5.4–5; Figure 5.2).

Flexible supports were most often used during foraging (85.71%). Stable supports were preferred during travel (46.94%) (Tables 5.4–5; Figure 5.2).

Table 5.4. Locomotor maintenance activities and support use by *R. avunculus* in Khau Ca Forest

	Forage		Travel		
	n	%	n	%	
Support number:					
Single	12	42.86%	645	77.43%	n.s.
Combined	10	35.71%	141	16.93%	n.s.
Multi	4	14.29%	35	4.20%	n.s.
Network	2	7.14%	12	1.44%	n.s.
Subtotal	*28*	*100.00%*	*833*	*100.00%*	
Support size:					
Trunk	1	3.57%	23	2.76%	n.s.
Bough	2	7.14%	149	17.89%	n.s.
Branch	18	64.29%	615	73.83%	n.s.
Twigs	6	21.43%	44	5.28%	n.s.
Liana	1	3.57%	2	0.24%	n.s.
Subtotal	*28*	*100.00%*	*833*	*100.00%*	
Support orientation:					
Horizontal	11	39.29%	378	45.38%	n.s.
Oblique	10	35.71%	298	35.77%	n.s.
Vertical	2	7.14%	111	13.33%	n.s.
Terminal	5	17.86%	33	3.96%	n.s.
Fork		0.00%	13	1.56%	n.s.
Subtotal	*28*	*100.00%*	*833*	*100.00%*	
Support flexibility:					
Flexible	24	85.71%	442	53.06%	n.s.
Stable	4	14.29%	391	46.94%	*
Subtotal	*28*	*100.00%*	*833*	*100.00%*	

Note. The last column represents significance of differences between frequencies of travel and forage after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Travel vs. forage: G (support number) = 16.190 **, G(support size) = 13.187 *, G(support orientation) = 8.882, n.s., G(support flexibility) = 13.113 ***.

Table 5.5. Locomotion and support use by *R. avunculus* in Khau Ca Forest

	Quadrupedalism		Leap		Climb		Drop		Arm-swing		Other locomotion		
	n	%	n	%	n	%	n	%	n	%	n	%	
<u>Support number:</u>													
Single	375	81.70%	101	75.37%	82	71.93%	51	56.04%	35	77.78%	13	72.22%	n.s.
Combined	69	15.03%	28	20.90%	12	10.53%	29	31.87%	8	17.78%	5	27.78%	n.s.
Multi	7	1.53%	3	2.24%	17	14.91%	10	10.99%	2	4.44%	-	-	***
Network	8	1.74%	2	1.49%	3	2.63%	1	1.10%	-	-	-	-	n.s.
Subtotal	*459*	*100.00%*	*134*	*100.00%*	*114*	*100.00%*	*91*	*100.00%*	*45*	*100.00%*	*18*	*100.00%*	
<u>Support number:</u>													
Trunk	6	1.31%	1	0.75%	14	12.28%	2	2.20%	1	2.22%	-	-	***
Bough	112	24.40%	24	17.91%	8	7.02%	2	2.20%	3	6.67%	2	11.11%	***
Branch	326	71.02%	99	73.88%	84	73.68%	75	82.42%	35	77.78%	14	77.78%	n.s.
Twig	15	3.27%	10	7.46%	5	4.39%	12	13.19%	6	13.33%	2	11.11%	*
Liana	-	-	-	-	3	2.63%	-	-	-	-	-	-	n.s.
Subtotal	*459*	*100.00%*	*134*	*100.00%*	*114*	*100.00%*	*91*	*100.00%*	*45*	*100.00%*	*18*	*100.00%*	
<u>Support orientation:</u>													
Horizontal	232	50.54%	65	48.51%	-	-	45	49.45%	24	53.33%	8	44.44%	n.s.
Oblique	215	46.84%	43	32.09%	22	19.30%	27	29.67%	15	33.33%	7	38.89%	*
Vertical	-	-	11	8.21%	89	78.07%	7	7.69%	3	6.67%	-	-	***
Terminal	10	2.18%	10	7.46%	-	-	9	9.89%	3	6.67%	3	16.67%	***
Fork	2	0.44%	5	3.73%	3	2.63%	3	3.30%	-	-	-	-	n.s.
Subtotal	*459*	*100.00%*	*134*	*100.00%*	*114*	*100.00%*	*91*	*100.00%*	*45*	*100.00%*	*18*	*100.00%*	
<u>Support flexibility:</u>													
Flexible	220	47.93%	74	55.22%	60	52.63%	70	76.92%	31	68.89%	11	61.11%	n.s.
Stable	239	52.07%	60	44.78%	54	47.37%	21	23.08%	14	31.11%	7	38.89%	*
Subtotal	*459*	*100.00%*	*134*	*100.00%*	*114*	*100.00%*	*91*	*100.00%*	*45*	*100.00%*	*18*	*100.00%*	

Note. The last column represents significance of differences between frequencies of locomotor behaviors and support use after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Locomotion vs. support use: G (support number) = 64.780 ***, G(support size) = 103.628 ***, G(support orientation) = 472.178 ***, G(support flexibility) = 32.023 ***.

Table 5.6. G-tests of independence in support use by locomotor behaviors of *R. avunculus* in Khau Ca Forest

	Support number	Support size	Support orientation	Support flexibility
Quadrupedalism vs. Leap	2.913 n.s.	6.222 n.s.	53.04 ***	2.210 n.s.
Quadrupedalism vs. Climb	31.908 ***	50.268 ***	418.583 ***	0.808 n.s.
Quadrupedalism vs. Drop	32.966 ***	40.759 ***	45.332 ***	26.985 ***
Quadrupedalism vs. Arm-swing	3.206 n.s.	14.783 **	19.045 ***	7.363 **
Quadrupedalism vs. Other	2.832 n.s.	4.105 n.s.	6.923 n.s.	1.211 n.s.
Leap vs. Climb	17.963 ***	27.293 ***	179.97 ***	0.167 n.s.
Leap vs. Drop	12.823 **	17.516 **	0.532 n.s.	11.423 ***
Leap vs. Arm-swing	1.881 n.s.	5.171 n.s.	3.203 n.s.	2.654 n.s.
Leap vs. Other	1.603 n.s.	1.008 n.s.	5.578 n.s.	0.225 n.s.
Climb vs. Drop	14.855 **	19.032 ***	155.734 ***	13.213 ***
Climb vs. Arm-swing	6.979 n.s.	9.882 *	113.058 ***	3.562 n.s.
Climb vs. Other	8.710 n.s.	6.386 n.s.	79.099 ***	0.454 *
Drop vs. Arm-swing	6.992 n.s.	1.594 n.s.	3.045 n.s.	0.997 n.s.
Drop vs. Other	4.687 n.s.	3.195 n.s.	4.633 n.s.	1.836 n.s.
Arm-swing vs. Other	1.986 n.s.	1.024 n.s.	3.553 n.s.	0.345 n.s.

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

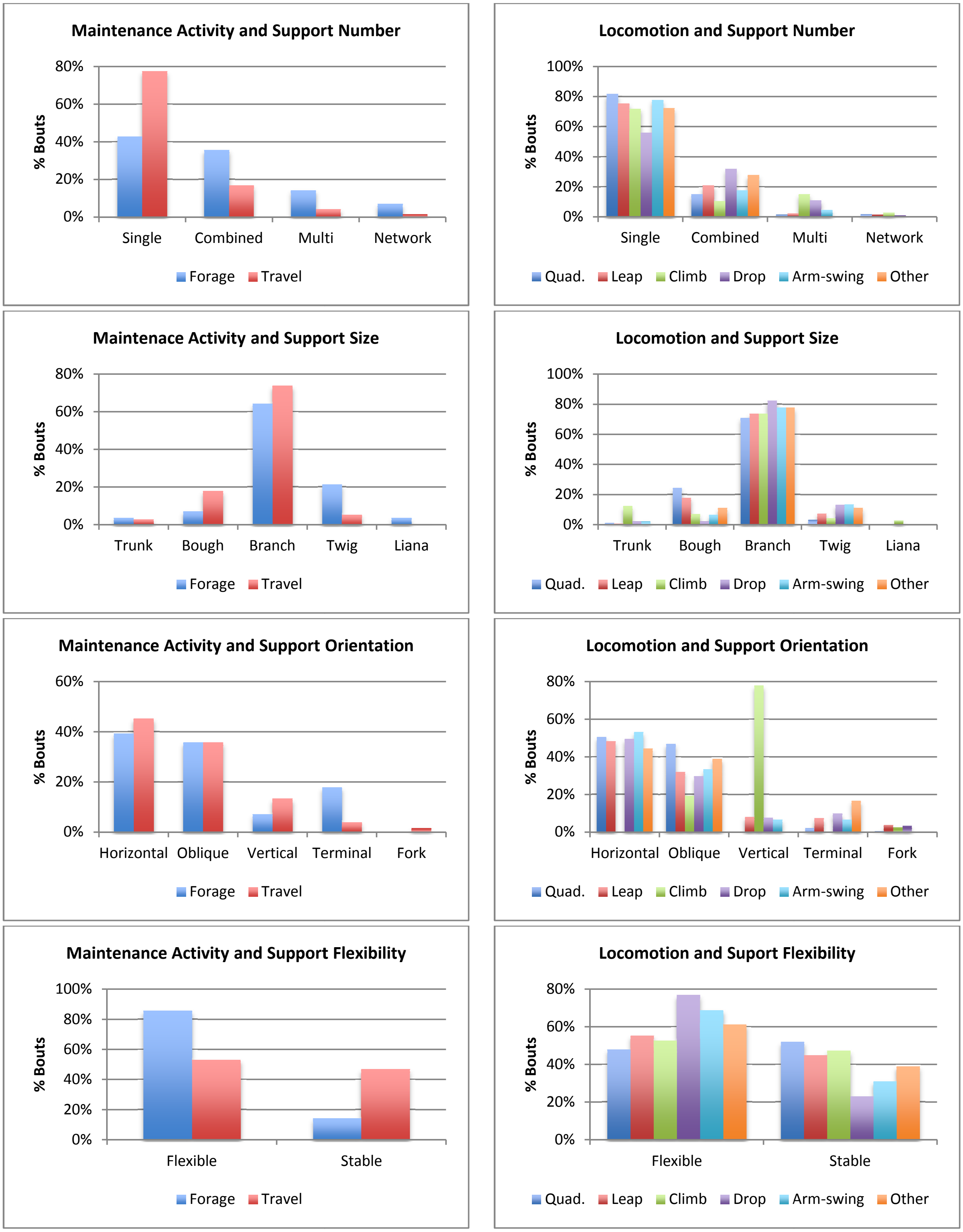

Figure 5.2. Frequencies of support use during maintenance activities and locomotor behaviors by *R. avunculus* in Khau Ca Forest

Note. Quad.: Quadrupedalism, Other: Other locomotion

5.3.3. Posture

There was significant independence in postures and associated maintenance activities (G = 99.258, p < 0.0001). Overall sit (81.13%) and stand (13.42%) were the most common postures for *R. avunculus* in Khau Ca Forest. Lie was most frequently used in social behaviors and rest. Cling was most frequent in display (Table 5.7 and Figure 5.3).

Table 5.7. Postural profiles of *R. avunculus* in Khau Ca Forest

	Rest		Feed		Display		Social behaviors		Overall postures		
	n	%	n	%	n	%	n	%	n	%	
Sit	675	82.22%	72	93.51%	16	43.24%	11	57.89%	774	81.13%	n.s
Stand	109	13.28%	-	-	18	48.65%	1	5.26%	128	13.42%	***
Lie	12	1.46%	-	-	1	2.70%	7	36.84%	20	2.10%	***
Cling	15	1.83%	-	-	2	5.41%	-	-	17	1.78%	n.s
Other	10	1.22%	5	6.49%	-	-	-	-	15	1.57%	n.s
Total	*821*	*100.00%*	*77*	*100.00%*	*37*	*100.00%*	*19*	*100.00%*	*954*	*100.00%*	

Note. The last column represents significance of differences between frequencies of maintenance activities by postural modes after comparisons using Bonferroni correction. n.s.: not significant, *** p < 0.001. All maintenance activities vs. postures: G = 99.258 ***.

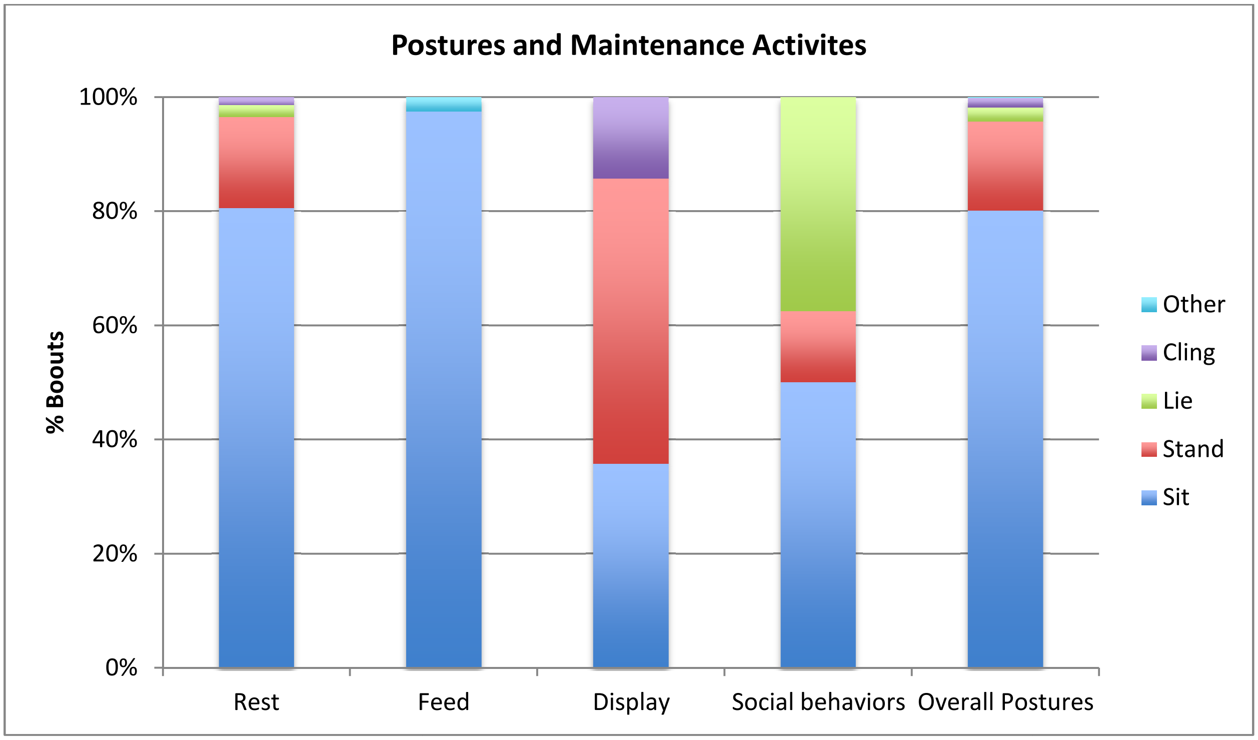

Figure 5.3. Frequencies of postural behaviors during rest, feed, display and social behaviors and overall by *R. avunculus* in Khau Ca Forest

5.3.4. Posture and Support Use

There was significant independence in associated maintenance activities and support use (Tables 5.8–9), and only significant independence in postural modes and used support orientation and flexibility by *R. avunculus* (Tables 5.10–11).

Single and combined supports were most frequently used by all postures and associated maintenance activities. *R. avunculus* only displayed and socialized on single and combined supports. Sit was most common on single supports (Tables 5.8 and 5.10; Figure 5.4).

Branches and boughs were most used during all postures and associated maintenance activities. Twigs and lianas were used more often during feeding than during other activities (Tables 5.8 and 5.10; Figure 5.4).

Horizontal and oblique supports were most often used by most postural modes and associated maintenance activities. Vertical supports were used during resting and displaying, and while clinging and other postures. Terminal supports were used more often in feeding and sitting than other activities and postures. Fork supports were used more often in resting and by siting than other activities and postures (Tables 5.8 and 5.10; Figure 5.4).

Flexible supports were most often used during feeding, while stable supports were most often used during resting, displaying, and social behaviors. Stable supports were preferred while sitting and lying, and flexible supports were preferred while standing, clinging and other postures (Tables 5.8 and 5.10; Figure 5.4).

Table 5.8. Postural maintenance activities and support use by *R. avunculus* in Khau Ca Forest

	Rest		Feed		Display		Social behaviors		
	n	%	n	%	n	%	n	%	
Support number:									
Single	726	88.43%	44	57.14%	32	86.49%	18	94.74%	n.s.
Combined	78	9.50%	16	20.78%	5	13.51%	1	5.26%	n.s.
Multi	9	1.10%	10	12.99%	-	-	-	-	***
Network	8	0.97%	7	9.09%	-	-	-	-	n.s.
Subtotal	*821*	*100.00%*	*77*	*100.00%*	*37*	*100.00%*	*19*	*100.00%*	
Support size:									
Trunk	4	0.49%	5	6.49%	1	2.70%	-	-	n.s.
Bough	184	22.41%	9	11.69%	8	21.62%	3	15.79%	n.s.
Branch	616	75.03%	47	61.04%	27	72.97%	16	84.21%	n.s.
Twig	16	1.95%	14	18.18%	1	2.70%	-	-	***
Liana	1	0.12%	2	2.60%	-	-	-	-	n.s.
Subtotal	*821*	*100.00%*	*77*	*100.00%*	*37*	*100.00%*	*19*	*100.00%*	
Support orientation:									
Horizontal	464	56.52%	39	50.65%	18	48.65%	8	42.11%	n.s.
Oblique	294	35.81%	24	31.17%	12	32.43%	9	47.37%	n.s.
Vertical	13	1.58%	-	-	1	2.70%	-	-	n.s.
Terminal	9	1.10%	9	11.69%	1	2.70%	-	-	***
Fork	41	4.99%	5	6.49%	5	13.51%	2	10.53%	n.s.
Subtotal	*821*	*100.00%*	*77*	*100.00%*	*37*	*100.00%*	*19*	*100.00%*	
Support flexibility:									
Flexible	319	38.86%	65	84.42%	19	51.35%	2	10.53%	***
Stable	502	61.14%	12	15.58%	18	48.65%	17	89.47%	***
Subtotal	*821*	*100.00%*	*77*	*100.00%*	*37*	*100.00%*	*19*	*100.00%*	

Note. The last column represents significance of differences between frequencies of maintenance activities by postural modes after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, *** $p < 0.001$. Overall maintenance vs. support use: G (support number) = 60.572 ***, G(support size) = 59.040 ***, G(support orientation) = 31.895 *, G(support flexibility) = 73.003 ***.

Table 5.9. G-tests of independence in support use by postural maintenance activities of *R. avunculus* in Khau Ca Forest

	Support number	Support size	Support orientation	Support flexibility
Overall	60.572 ***	59.04 ***	31.895 **	73.003 ***
Rest vs. Feed	55.368 ***	55.719 ***	24.383 ***	62.356 ***
Rest vs. Display	2.041 n.s.	1.846 n.s.	4.756 n.s.	2.261 n.s.
Rest vs. Social behaviors	1.280, n.s.	1.568, n.s.	3.238 n.s.	7.574 **
Feed vs. Display	17.191 ***	10.324 *	6.409 n.s.	13.500 ***
Feed vs. Social behaviors	13.211 **	10.626 *	5.586 n.s.	38.198 ***
Display vs. Social behaviors	0.994 n.s.	2.087 n.s.	2.588 n.s.	10.042 *

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 5.10. Postures and support use by *R. avunculus* in Khau Ca Forest

	Sit		Stand		Lie		Cling		Other posture		
	n	%	n	%	n	%	n	%	n	%	
Support number:											
Single	665	85.92%	113	88.28%	17	85.00%	14	82.35%	11	73.33%	n.s.
Combined	85	10.98%	9	7.03%	3	15.00%	2	11.76%	1	6.67%	n.s.
Multi	14	1.81%	3	2.34%	-	-	1	5.88%	1	6.67%	n.s.
Network	10	1.29%	3	2.34%	-	-	-	-	2	13.33%	n.s.
Subtotal	*774*	*100.00%*	*128*	*100.00%*	*20*	*100.00%*	*17*	*100.00%*	*15*	*100.00%*	
Support size:											
Trunk	7	0.90%	1	0.78%		0.00%	2	11.76%	-	-	n.s.
Bough	172	22.22%	24	18.75%	7	35.00%	1	5.88%	-	-	n.s.
Branch	570	73.64%	96	75.00%	13	65.00%	13	76.47%	14	93.33%	n.s.
Twig	23	2.97%	6	4.69%	-	-	1	5.88%	1	6.67%	n.s.
Liana	2	0.26%	1	0.78%	-	-	-	-	-	-	n.s.
Subtotal	*774*	*100.00%*	*128*	*100.00%*	*20*	*100.00%*	*17*	*100.00%*	*15*	*100.00%*	
Support orientation:											
Horizontal	428	55.30%	83	64.84%	11	55.00%	2	11.76%	5	33.33%	n.s.
Oblique	282	36.43%	40	31.25%	9	45.00%	2	11.76%	6	40.00%	n.s.
Vertical	-	-	-	-	-	-	12	70.59%	2	13.33%	***
Terminal	15	1.94%	4	3.13%	-	-	-	-	-	-	n.s.
Fork	49	6.33%	1	0.78%	-	-	1	5.88%	2	13.33%	n.s.
Subtotal	*774*	*100.00%*	*128*	*100.00%*	*20*	*100.00%*	*17*	*100.00%*	*15*	*100.00%*	
Support flexibility:											
Flexible	309	39.92%	68	53.13%	3	15.00%	11	64.71%	14	93.33%	*
Stable	465	60.08%	60	46.88%	17	85.00%	6	35.29%	1	6.67%	*
Subtotal	*774*	*100.00%*	*128*	*100.00%*	*20*	*100.00%*	*17*	*100.00%*	*15*	*100.00%*	

Note. The last column represents significance of differences between frequencies of postural behaviors and support use after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Postures vs. support use: G (support number) = 12.719 n.s., G(support size) = 23.173 n.s., G(support orientation) = 134.267 ***, G(support flexibility) = 36.096 ***.

Table 5.11. G-tests of independence in support use by postural behaviors of *R. avunculus* in Khau Ca Forest

	Support number	Support size	Support orientation	Support flexibility
Overall	12.719 n.s.	23.173 n.s.	134.267 ***	36.096 ***
Sit vs Stand	2.784, n.s.	2.281 n.s.	12.313 *	7.765 **
Sit vs Lie	1.483 n.s.	3.051 n.s.	3.630 n.s.	5.794 *
Sit v Cling	1.409 n.s.	9.453 n.s.	105.109 ***	4.148 **
Sit vs Other	7.114 n.s.	8.155 n.s.	18.836 ***	19.043 ***
Stand vs Lie	2.89 n.s.	4.438 n.s.	2.630 n.s.	11.075 ***
Stand vs Cling	1.734 n.s.	7.176 n.s.	66.999 ***	0.826 n.s.
Stand vs other	3.995 n.s.	6.413 n.s.	18.18 **	10.852 ***
Lie vs Cling	1.635 n.s.	8.977 *	29.456 ***	10.099 **
Lie vs other	5.784 n.s.	10.411 *	7.738 n.s.	24.235 ***
Cling vs other	3.348 n.s.	4.071 n.s.	11.561 *	4.198 *

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

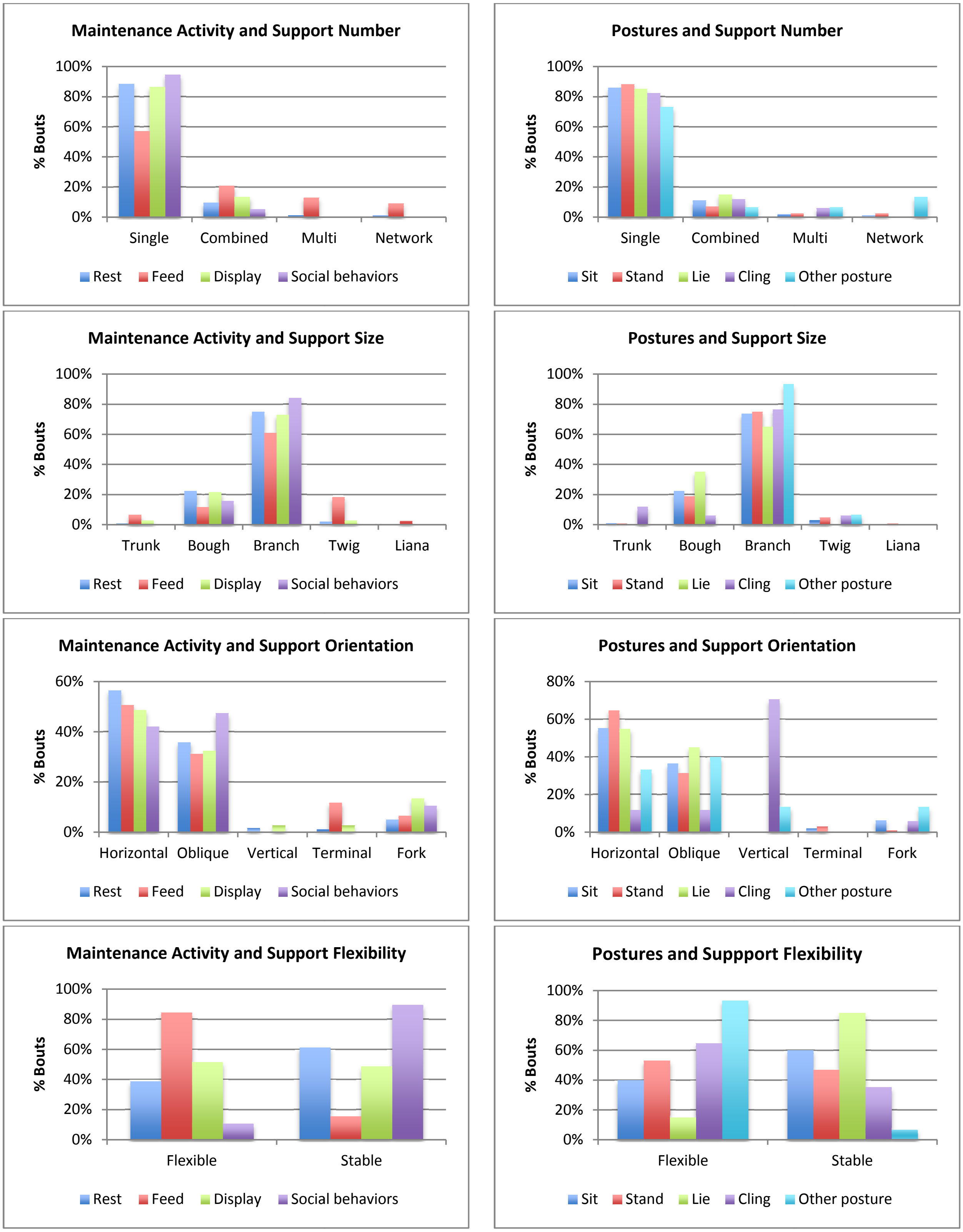

Figure 5.4. Frequencies of supports use during maintenance activities and postural behaviors by *R. avunculus* in Khau Ca Forest

5.4. Discussion

During this study, adult male Tonkin snub-nosed monkeys (*R. avunculus*) were only recorded using arboreal supports for traveling, foraging, feeding, resting, displaying and social behaviors. Dong Thanh Hai (2011) also reported that *R. avunculus* rarely spent time on the ground with only six observations of terrestrial behavior over several months of observations. This suggests that *R. avunculus* is possibly the most arboreal species of *Rhinopithecus* since all of the Chinese snub-nosed monkeys are partly terrestrial (see Bleisch *et al.*, 1993; Grueter *et al.*, 2013; Kirkpatrick and Long, 1994; Li, 2007; Wu, 1993). At present there is no information available on the amount of time spent in trees and on the ground for the newly described snub-nosed monkey, *R. strykeri* from Myanmar (Geissmann *et al.*, 2011; Long *et al.*, 2012).

The locomotor repertoire of adult male *R. avunculus* is dominated by quadrupedal walking and running (53.31%), leaping (15.56%), climbing (13.24%), and dropping (10.57%) while its postural repertoire is dominated by sitting (81.13%) and standing (13.42%). During traveling and foraging, *R. avunculus* often walked and ran quadrupedally on single and horizontal/oblique branches. During resting, feeding, displaying, and social behaviors, *R. avunculus* frequently used sitting and standing on single/combined, horizontal/oblique, and stable bough and branches.

R. avunculus are larger than most colobines. Thus, I hypothesized that larger-bodied *R. avunculus* would leap, suspend and climb more frequently, and quadrupedal run and walk less frequently compared to other colobines based on the research of Cartmill and Milton (1977), Crompton (1983), and Fleagle and Mittermeier (1980). However, my study results do not support this hypothesis. I found *R. avunculus* predominately used quadrupedal walking and running which accounted for > 50% of overall locomotion; such high frequencies of quadrupedalism had more often been observed in smaller-bodied African colobines. A different pattern is seen in comparison with a number of the smaller Asian colobines including *Presbytis melalophos* (Fleagle, 1978), *T. francois* and *T. leucocephlus* (Xiong *et al.*, 2009; Zhou *et al.*,

2013) animals that use quadrupedal walking and running less frequently that *R. avunculus* (see detailed in Table 5.12).

Leaping accounted for 15.85% of travel by *R. avunculus* which is consistent with frequencies reported for African colobines and *Pygathrix nigripes* but lower than smaller-bodied Asian colobines: *Presbytis melalophos*, *Trachypithecus francoisi* and *T. leucocephalus* (Table 5.12). The results for colobines did not support Fleagle and Mittermeier's (1980) findings that suggested smaller species leap more than larger species (see Gebo and Chapman, 1995b; McGraw, 1998a). One exception is *T. delacouri* which only infrequently leaped during travel and foraging. It should also be noted, however that *T. delacouri* is coping with a highly degraded limestone habitat with poor quality forest at Van Long Nature Reserve (Workman and Schmitt, 2012).

R. avunculus more frequently climbed than smaller-bodied Asian colobines including *Presbytis melelophos*, *Pygathrix nigripes* and *Trachypithecus obscurus*, and less frequently than Asian colobines, *Trachypithecus delacouri* and *T. francoisi* (Table 5.12). High frequencies of climbing during foraging by *R. avunculus* are possibly associated with its food items (leaves and fruit) distributed in the periphery of trees. Dong Thanh Hai (2011) reported *R. avunculus* spent 12% of their feeding time in the upper canopy.

There was no report of dropping in African colobines (Table 5.12). During travel and foraging, *R. avunculus* drop more frequently than other Asian colobines. *R. avunculus* and *Pygathrix nigripes*, and climbed more frequently than *Trachypithecus*. This is possibly explained by differences of habitat architecture because animals can only drop on safe arboreal substrates. *R. avunculus* and *Pygathrix nigripes* inhabit relatively undisturbed and dense forests where there are many forest layers and arboreal substrates that can bear the animal's weight. In contrast, *Trachypithecus francoisi* and *T. leucocephalus* live in degraded forest on limestone and they used free falling (=drop) during fast traveling from hilltop down to base of the hill (Xiong *et al*., 2009).

Table 5.12. Locomotor profiles of Asian and African colobines

	Body size (kg)*		Quadrupedalism						
		Activity	Walk	Run	Leap	Climb	Drop	Suspension	Other
Colobus badius[1]	M: 8.3; F: 8.2	Overall	53.1%	8.2%	17.8%	17.0%	-	3.9%	-
		Travel	54.8%	9.3%	20.8%	12.2%	-	2.9%	-
		Forage	53.4%	5.0%	15.0%	21.6%	-	5.0%	-
Colobus badius[2]	M: 8.2; F: 8.2	Travel	34.0%		30.0%	29.0%	-	-	7.0%
		Forage	44.0%		16.0%	37.0%	-	-	3.0%
Colobus guereza[2]	M: 10.1; F: 8.2	Travel	39.0%		44.0%	11.0%	-	-	6.0%
		Forage	43.0%		33.0%	18.0%	-	-	6.0%
Colobus guereza[3]	M: 10.1; F: 8.2	Overall	42.08%		39.49%	17.63%	-	1.29%	4.51%
Colobus polykomos[1]	M: 9.9; F: 8.3	Overall	41.8%	29.4%	14.5%	14.3%	-	-	-
		Travel	42.6%	31.8%	17.6%	8.0%	-	-	-
		Forage	50.5%	12.0%	13.3%	24.2%	-	-	-
Colobus versus[1]	M: 4.6; F: 4.2	Overall	45.2%	22.4%	20.4%	12.0%	-	-	-
		Travel	39.1%	29.6%	25.0%	6.3%	-	-	-
		Forage	54.5%	10.5%	13.5%	20.8%	-	-	-
Presbytis melalophos[4]	M: 6.6; F: 6.5	Overall	20.7%		67.5%	8.4%	-	3.4%	-
Pygathrix nigripes[5]	M: 11.0; F: 9.0	Travel	61.0%	-	17.0%	8.0%	4.0%	10.0%	-
R. avunculus[6]	M: 14.5; F: 8.5	Overall	53.31%		15.56%	13.24%	10.57%	5.23%	2.09%
		Travel	52.7%		15.85%	13.21%	10.68%	5.4%	2.16%
		Forage	71.43%		7.14%	14.29%	7.14%	-	-
Trachypithecus delacouri[7]	M: 8.6; F: 7.8	Travel	65.0%		6.0%	28.0%	-	-	1.0%
		Forage	77.0%		10.0%	12.0%	-	-	1.0%
Trachypithecus francosi[8]	M: 8.0; F: 7.2	Overall	19.9%	11.2%	43.3%	25.5%	-	-	-
Trachypithecus francosi[9]	M: 8.0; F: 7.2	Overall	34.1%		46.3%	13.4%	3.1%	1.6%	1.5%
Trachipythecus leucocephalus[9]	M: 8.0; F: 7.8	Overall	30.6%		47.3%	19.7%	1.6%	0.5%	0.3%
Trachypithecus obscurus[4]	M: 7.9; F: 6.2	Overall	50.6%		43.0%	9.2%	-	-	3.4%

Note. * Body size followed by Rowe and Myers (2014), M = Male, F = Female. [1] McGraw (1998a), [2] Gebo and Chapman (1995b), [3] Morbeck (1977), [4] Fleagle (1978), [5] Rawson (2009), [6] In this study, [7] Workman and Schmitt (2012), [8] Zhou *et al.* (2013), [9] Xiong *et al.* (2009).

During travel, arm-swing accounted 5.4% for *R. avunculus* which was less than *Pygathrix nigripes* but more frequent than other African and Asian colobines (Table 5.12). Suspensory locomotion in African colobines was only reported for *Colobus badius* (McGraw, 1998a) and *C. guereza* (Morbeck, 1977). Among *Trachypithecus* species, there were only reports of arm-swing by *T. leucocephalus* and *T. francoisi* at low frequencies of 0.5% and 1.6% (Xiong *et al.*, 2009). Suspensory locomotion was reported for *Pygathrix nemaeus* in captivity by Byron and Covert (2004), Workman and Covert (2005), andWright *et al.* (2008). Comparison among colobines, suspensory data on *R. avunculus* and other odd-nosed monkeys (*P. nigripes* and *P. nemaeus*) support the hypothesis that larger-bodied primates use suspensory locomotion more frequent than so smaller-bodied primates (Fleagle and Mittermeier, 1980).

Similar to other colobines, sitting was the most frequent posture overall, and during all maintenance activities by *R. avunculus* (Table 5.13). In comparison with African and Asian colobines, my results did not support the hypothesis of larger-bodied animals sitting more frequently than do smaller-bodied animals. As noted in Chapter II, McGraw (1998b) identified some basic differences between postural activities between colobines and cercopithecines with the former sitting more frequently than the latter. He argued that this was in part explained by the tendency of colobines to feed while sitting. In contrast he noted that cercopithecines often feed while in a quadrupedal stand.

Quadrupedal stand accounted for more than 13% of overall postures and resting by *R. avunculus* in higher frequencies than reported for African and other Asian colobines (Table 5.13). In this study, I did not record adult male *R. avunculus* feeding while standing but did see adult females and juveniles doing so (see chapters VI and VII). Similar to other arboreal colobines, *R. avunculus* used standing less frequently than semiterrestrial colobines like *R. bieti* (Grueter *et al.*, 2013) and *Trachypithecus delacouri* (Workman and Schmitt, 2012).

Table 5.13. Postural profiles of Asian and African colobines

	Body size (kg)*	Activity	Sit	Stand	Lie	Cling	Other
Colobus badius[1]	M: 8.3; F: 8.2	Overall	87.0%	1.4%	10.3%	-	1.3%
		Resting	80.4%	-	19.6%	-	-
		Feeding	97.3%	0.17%	-	-	1.53%
		Social	72.5%	13.5%	13.2%	-	0.8%
Colobus badius[2]	M: 8.3; F: 8.2	Travel	56.0%	41.0%	1.0%	1.0%	1.0%
		Feed	71.0%	23.0%	3.0%	< 1.0%	< 3.0%
Colobus guereza[2]	M: 10.1; F: 8.2	Travel	94.0%	5.0%	1.0%	1.0%	-
		Feed	86.0%	4.0%	10.0%	< 1.0%	< 1.0%
Colobus guereza[3]	M: 10.1; F: 8.2	Overall	80.56%	2.1%	13.01%	1.55%	2.78%
Colobus polykomos[1]	M: 9.9; F: 8.3	Overall	89.5%	0.19%	9.2%	-	1.11%
		Resting	82.8%	-	17.2%	-	-
		Feeding	97.3%	0.41%	-	-	2.29%
		Social	80.1%	-	19.9%	-	-
Colobus versus[1]	M: 4.6; F: 4.2	Overall	90.7%	1.3%	7.5%	-	0.05%
		Resting	86.9%	-	13.1%	-	-
		Feeding	98.3%	0.72%	-	-	0.98%
		Social	81.0%	9.5%	7.6%	-	1.9%
Presbytis melalophos[4]	M: 6.6; F: 6.5	Overall	93.0%	-	-	-	7.0%
R. avunculus[6]	M: 14.5; F: 8.5	Overall	81.13%	13.42%	2.1%	1.78%	1.57%
		Resting	82.22%	13.28%	1.46%	1.83%	1.22%
		Feeding	93.51%	-	-	-	6.49%
		Social	57.89%	5.26%	36.84%	-	-
Rhinopithecus bieti[7]	M: 35.0; F: 9.0	Resting	74.0%	-	4.0%	-	22.0%
		Feeding	84.0%	7.0%	2.0%	1.0%	6.0%
Trachypithecus delacouri[8]	M: 8.6; F: 7.8	Resting	98.0%	< 1%	1.0%	-	< 1.0%
		Feeding	95.0%	5.0%	-	-	< 1.0%
		Social	71.0%	22.0%	7.0%	-	-
Trachypithecus obscurus[4]	M: 7.9; F: 6.2	Overall	98.0%	-	-	-	2.0%

Note. * Body size followed by Rowe and Myers (2014): M = Male, F = Female. [1] McGraw (1998b), [2] Gebo and Chapman (1995b), [3] Morbeck (1977), [4] Fleagle (1978), [5] Rawson (2009), [6] In this study, [7] Grueter *et al.* (2013), [8] Workman and Schmitt (2012), [9] Zhou *et al.* (2013).

Lie, cling and other postures (bipedal stand and forelimb-suspend) were used less often by *R. avunculus* and other arboreal colobines as well (Table 5.13). Lie was used often during resting and social behaviors, especially when grooming each other. Cling and other postures were used occasionally during feeding and resting. Grueter *et al.* (2013) reported *R. bieti* used hunching 22% if the time during resting and this was provisionally hypothesized as a particular energy-saving posture during cool wet season (Dasilva, 1993; Grueter *et al.*, 2013). I observed *R. avunculus* using sit-huddling during resting during the cool (and dry) season at Khau Ca.

R. avunculus used single supports most frequently, followed by combined, multi and network supports during overall activities, locomotion and postures. Branches and boughs were the most preferred substrates. Trunks, twigs and lianas were seldom used, but they were used most frequently during resting and foraging (Table 5.14). During this study, I did not record *R. avunculus* on the ground (and they have only been observed on the ground a handful of occasions during all field observations [Dong Thanh Hai, 2011]). In contrast a number of Asian colobines have been observed to spend substantial amounts of time on the ground: 19.5% by *R. bieti* (Grueter *et al*., 2013), 46.7% by *T. francoisi* on the ground (Zhou *et al.*, 2013), 39.2% and 30.0% by *T. francoisi* and *T. leucocephalus* respectively (Xiong *et al.*, 2009), and extremely high, more than 80% of locomotion and postures by *T. delacouri* (Workman and Schmitt, 2012). It is also widely reported that some species of *Semnopithecus* spend a substantial amount of time on the ground (Fleagle, 2013; Fleagle, 1999; Ripley, 1967). McGraw (1998b) reported on infrequent use of the ground by *Colobus badius*, *C. polykomos* and *C. versus* while Gebo and Chapman (1995b) and Morbeck (1977) did not record ground use by colobines in their studies.

Table 5.14. Support size used by Asian and African colobines

	Body size (kg)*	Activity	Ground	Trunk	Bough (Large)	Branch (Medium)	Twig (Small)	Liana (Other)
Colobus badius[1]	M: 8.3; F: 8.2	Locomotion	0.14%	1.3%	38.6%	28.6%	31.5%	-
		Posture	0.17%	-	47.1%	35.6%	17.1%	0.08%
Colobus badius[2]	M: 8.3; F: 8.2	Overall	-	-	14.0%	68.0%	18.0%	-
		Locomotion	-	-	14.0%	68.0%	18.0%	-
		Posture	-	-	13.0%	67.0%	20.0%	-
Colobus guereza[2]	M: 10.1; F: 8.2	Overall	-	-	23.0%	61.0%	16.0%	-
		Locomotion	-	-	22.0%	62.0%	16.0%	-
		Posture	-	-	25.0%	59.0%	16.0%	-
Colobus guereza[3]	M: 10.1; F: 8.2	Overall			19.9%	58.07%	22.4%	-
		Locomotion	-	-	20.75%	61.30%	17.5%	-
		Posture	-	-	18.87%	58.01%	23.12%	-
Colobus polykomos[1]	M: 9.9; F: 8.3	Locomotion	0.4%	0.6%	48.3%	25.7%	25.0%	-
		Posture	0.16%	-	38.1%	40.1%	21.6%	0.04%
Colobus versus[1]	M: 4.6; F: 4.2	Locomotion	5.5%	1.7%	24.2%	38.1%	30.3%	0.2%
		Posture	0.95%	-	24.2%	49.8%	23.8%	1.25%
Presbytis melalophos[4]	M: 6.6; F: 6.5	Feeding	-	-	13.0%	75.0%	12.0%	-
Pygathrix nigripes[5]	M: 11.0; F: 9.0	Overall	-	0.1%	14.3%	73.4%	12.2%	-
		Travelling	-	1.4%	16.1%	71.1%	11.4%	-
		Feeding	-	-	6.1%	68.0%	25.9%	-
		Inactive	-	0.0%5	17.3%	74.7%	7.9%	-

Table 5.14 (continued)

	Body size (kg)*	Activity	Ground	Trunk	Bough (Large)	Branch (Medium)	Twig (Small)	Liana (Other)
R. avunculus[6]	M: 14.5; F: 8.5	Overall	-	1.87%	19.56%	73.77%	4.46%	0.33%
		Locomotion	-	2.79%	17.54%	73.52%	5.81%	0.35%
		Posture	-	1.05%	21.38%	74.00%	3.25%	0.31%
		Travel	-	2.76%	17.89%	73.83%	5.28%	0.24%
		Forage	-	3.57%	7.14%	64.29%	21.43%	3.57%
		Rest	-	6.49%	11.69%	61.04%	18.18%	2.60%
		Feed	-	0.49%	22.41%	75.03%	1.95%	0.12%
		Display	-	-	15.79%	84.21%	-	-
		Social behaviors		2.70%	21.62%	72.97%	2.70%	-
Rhinopithecus bieti[7]	M: 35.0; F: 9.0	Overall	19.5%			80.5%		
		Arboreal postures	-	6.0%	23.0%	62.0%	9.0%	-
		Resting	-	8.6%	30.3%	55.8%	5.3%	-
		Feeding	-	0.7%	16.8%	66.2%	16.3%	-
Trachypithecus francoisi[8]		Locomotion	46.7%			53.3%		
Trachypithecus francoisi[9]		Overall	39.2%			60.8%		
Trachypithecus leucocephalus[9]		Overall	30.0%			70.0%		
Trachypithecus delacouri		Overall	> 80.0%			< 20.0%		
Trachypithecus obscurus[4]	M: 7.9; F: 6.2	Feeding	-	-	28.0%	67.0%	5.0%	-

Note. * Body size followed by Rowe and Myers (2014), M = Male, F = Female. [1] McGraw (1998b), [2] Gebo and Chapman (1995b), [3] Morbeck (1977), [4] Fleagle (1978), [5] Rawson (2009), [6] In this study, [7] Grueter *et al*. (2013), [8] Zhou *et al*. (2013), [9] Xiong *et al*. (2009).

Table 5.15. Support orientation used by Asian and African colobines

	Body size (kg)*	Activity	Horizontal	Oblique	Vertical	Terminal	Fork
Colobus badius[1]	M: 8.3; F: 8.2	Overall	46.0%	50.0%	4.0%	-	-
		Locomotion	42.0%	52.0%	6.0%	-	-
		Posture	52.0%	47.0%	1.0%	-	-
Colobus guereza[1]	M: 10.1; F: 8.2	Overall	48.0%	49.0%	3.0%	-	-
		Locomotion	46.0%	50.0%	4.0%	-	-
		Posture	52.0%	45.0%	3.0%	-	-
Colobus guereza[2]	M: 10.1; F: 8.2	Overall	35.63%	60.77	1.15%	-	2.45%
		Locomotion	36.64%	60.76%	0.26%	-	2.34%
		Posture	36.28%	60.99%	0.21%	-	2.72%
R. avunculus[3]	M: 14.5; F: 8.5	Overall	49.75%	36.80%	6.67%	3.14%	3.64%
		Overall locomotion	43.44%	38.21%	12.78%	4.07%	1.51%
		Overall posture	55.45%	35.53%	1.47%	1.99%	5.56%
		Travel	43.58%	38.30%	12.61%	3.96%	1.56%
		Forage	39.29%	35.71%	7.14%	17.86%	-
		Feed	50.65%	31.17%	-	11.69%	6.49%
		Rest	56.52%	35.81%	1.58%	1.10%	4.99%
		Display	48.65%	32.43%	2.70%	2.70%	13.51%
		Social behaviors	42.11%	47.37%	-	-	10.53%
Rhinopithecus bieti[4]	M: 35.0; F: 9.0	Rest	68.6%	27.8%	3.6%	-	-
		Feed	45.2%	33.6%	21.2%	-	-

Note. * Body size followed by Rowe and Myers (2014), M = Male, F = Female. [1] Gebo and Chapman (1995b), [2] Morbeck (1977), [3] In this study, [4] Grueter *et al*. (2013).

R. avunculus used horizontal and oblique supports most frequently in all activities, but lower frequencies than other colobines (Table 5.15). In comparison with African colobines, both *R. avunculus* (in this study) and *R. bieti* (Grueter *et al*., 2013) used vertical supports more frequently during locomotion (e.g., climbing) and postures (e.g., cling). *R. avunculus* used terminal supports (twigs) more frequent during foraging and feeding because their main dietary items (e.g., young leaves, leaf petioles and fruits) are distributed in the periphery of tree crown. There were no reports on vertical support use in other studies (e.g., Gebo and Chapman, 1995b; Grueter *et al.*, 2013; Morbeck, 1977) and this might be explained by different methodologies to categorize and collect data on support orientation. *R. avunculus* used forks more frequently in postural behaviors than locomotion (travel). The only other report of the use of forks was Morbeck's (1977) study in a riparian forest in Kenya where she reported *Colobus guereza* used "crotch" (fork) for more than 2% of locomotion and postures.

In summary, my results indicated that Tonkin snub-nosed monkeys are arboreal, with quadrupedalism, leaping and climbing being their dominant locomotor modes while sitting and standing were their main postural modes. *R. avunculus* often used single and combined supports. Branches and boughs were used most frequently during locomotion and postures. Horizontal and oblique supports were used in all activities. In comparison to other colobines, my results only support a part of the hypotheses of body size effects in primate positional behavior. Further analyses and comparisons in the next chapters provide more understanding of factors that affect positional behavior and support use of Tonkin snub-nosed monkeys in Khau Ca Forest.

Summary

- Adult male Tonkin snub-nosed monkeys exhibited a total of nine locomotor modes (19 submodes) and six postural modes (16 submodes). There was significant independence in positional behaviors and maintenance activities, and positional and support use by *R. avunculus.*

- Locomotor repertoire of adult male *R. avunculus* included quadrupedalism most frequently, followed by leap, climb, drop, arm-swing and other locomotion. There was no significant independence in locomotor behaviors and associated maintenance activities (travel and forage) employed by *R. avunculus*. Quadrupedalism dominated all activities during travel and foraging. Leap, climb and drop were used much more frequently during travel than during foraging. Arm-swing was used only during travel.
- Postural repertoire of adult male *R. avunculus* included sitting most frequently, followed by stand, lie, cling and other posture. There was significant independence in postures and associated maintenance activities and sit and stand were the most common postures overall, lie was most frequent in social behaviors and rest, and cling was most frequent in display of *R. avunculus* in Khau Ca Forest.
- There were significant differences in associated maintenance activities, positional behaviors and support use by *R. avunculus*. During associated maintenance activities, *R. avunculus* most frequently used single and combined supports of branches and boughs on horizontal and oblique orientation. Flexible supports were most often used during foraging and feeding while stable supports were preferred during travel, resting and other activities.
- Comparison to other studied colobines, the positional behavior data of *R. avunculus* provides evidences of complexity of body size effects in positional behavior and support use of African and Asian colobines.

CHAPTER VI

DIFFERENCES BETWEEN ADULT MALES AND ADULT FEMALES

6.1. Introduction

Primate males and females often differ in their body size, the nutritional cost of reproduction, and social behaviors, therefore significant sex-based differences in positional behavior might be expected (Garber, 2011). Doran (1993) argued that the presence of extensive variation in the positional behavior of sexually dimorphic living species might have important implications for contrasting sex-based behavioral patterns in our early hominid relatives. It is possible, for example, that if intraspecific morphological differences can be tied to intraspecific differences in behavior for males and females in living species, then such associations could shed light on differing roles of males and females in extinct primate communities (i.e., the roles of each sex in foraging, territorial defense, etc.). Differentiating male and female positional behavior patterns in living species is therefore important not just for understanding modern behavioral variation, but also for offering new avenues of inquiry into the life history of past species.

Increasingly, sex-based differences in positional behavior among primates have received the attention of researchers, e.g., Cant (1987), Chatani (2003), Doran (1993), Fan *et al.* (2013), Gebo (1992), Gebo and Chapman (1995b), Prates and Bicca-Marques (2008), Remis (1995), Sugardjito and Vanhooff (1986), Workman and Schmitt (2012), and Xiong *et al.* (2009). Available results for New and Old World monkeys, and great apes indicate that differences between adult males and females in positional behavior are subtle to none. For example, Cant (1987) reported the differences between adult male and female Sumatran orangutans (*Pongo* *pygmaeus*) in arboreal positional behavior and substrate use, but his results showed that smaller-sized females more frequently used suspensory postures than did larger-sized males. Doran (1993) found that the modestly dimorphic common chimpanzee (*Pan troglodytes*) had "no significant sex differences in the frequency of locomotor activities performed during either feeding or travel" (p. 102). Remis (1998) reported that there were sex-based differences in positional behavior and substrate use of western lowland gorilla (*Gorilla gorilla gorilla*) and she argued these differences were related more to social interactions and social role of adult males and females than to effects of their body size. Gebo (1992) reported no differences between sex classes of two New World monkeys, *Alouatta palliata* and *Cebus capucinus*. Similarly, Gebo and Chapman (1995b) also found no significant sex-based differences in positional behavior and support use among five sympatric Old World monkeys in Kibale Forest, Uganda. Among Asian colobines, Grueter *et al.* (2013) reported adult male and female *Rhinopithecus bieti* differed significantly in postural behavior and support use; and Xiong *et al.* (2009) reported sex-based differences in locomotion of *Trachypithecus francoisi* and *T. leucocephalus.* However, Workman and Schmitt (2012) found no significant differences for male and female *T. delacouri*. Thus, much of data indicated that primate males and females are highly conservative in positional behavior and support use (Garber, 2011).

In this chapter, I compare adult male and adult female behaviors for *R. avunculus* in Khau Ca Forest to identify sex-based differences in overall locomotor and postural behaviors in the context of different associated maintenance activities.

Hypotheses to test are as follows:

Hypothesis 6.1: Similar to other primates, larger-bodied adult male and smaller-bodied adult female *R. avunculus* do not differ significantly from one another in locomotion, postures, and support use.

This hypothesis is based on findings by Doran (1993), Gebo (1992), Gebo and Chapman (1995b), and Workman and Schmitt (2012) that reported there were no significant differences in positional behavior and support use by adult males and females.

<u>Hypothesis 6.2:</u> If Hypothesis 6.1 is not supported because of sexual dimorphism in *R. avunculus*, adult males with larger body mass, will more frequently use climbing and suspensory behavior, and will less frequently leap than adult females with smaller body mass; males will more frequently use sitting and standing behaviors, and less frequently use bipedal stand and cling.

This hypothesis is based on Fleagle and Mittermeier's (1980) hypothesis of body size effects in positional behavior and support use. This hypothesis was supported by studies of Cant (1987), Chatani (2003), Doran (1993), Fan *et al.* (2013), Gebo (1992), Gebo and Chapman (1995b), Prates and Bicca-Marques (2008), Remis (1995), Sugardjito and Vanhooff (1986), Workman and Schmitt (2012), and Xiong *et al.* (2009).

<u>Hypothesis 6.3:</u> If Hypothesis 6.1 is not supported, given larger-body size, adult males will use larger substrates more commonly than females; also, while foraging in smaller substrates males will more commonly use suspensory postures than females.

Similar to Hypothesis 6.2, this hypothesis is based on Fleagle and Mittermeier's (1980) findings about body size effects in support use by primates that were supported by Cant (1987), Fan *et al.* (2013), and Sugardjito and Vanhooff (1986).

To test these hypotheses as mentioned above, the question addressed in this chapter is:

- Do adult male and female *R. avunculus* differ in the frequencies of locomotor and postural behaviors and support use in Khau Ca Forest?

6.2. Methods

To compare male and female locomotor and postural profiles of *R. avunculus* in the Khau Ca Forest, I used the bout sampling technique described in Chapter III. Given that I was unable to identify individual members of the *R. avunculus* population in Khau Ca Forest, it would be inappropriate to pool all male and all female positional behavior for each age categories. Thus, I compared positional behavior profiles only for adult males and adult females.

For adult *R. avunculus*, sex differences in body mass and body proportions were clear from visual observation (see Table 2.3, Figure 6.1). Adult males are the largest members of a group with a robust head and large body, bluish face skin, thick pink lips, orange throat, black penis, and a tail with curly fur that is much longer than body and head. Adult females are large individuals (although smaller than adult males), have a slimmer body than adult male, dark bluish to dark face skin, big and black nipples and a tail white with smooth fur. Adult females with dependent offspring were also included in the adult female category (Lone adult females vs. Adult female with dependent offspring in locomotion: G = 6.043 n.s).

Following Doran (1993) and Remis (1995) I compared profiles for all postures and all locomotor behaviors and support use between adult male and adult female (including adult female with infant) *R. avunculus* in Khau Ca Forest using the G-test of independence. All tests were two-tailed and performed using Microsoft Excel (see MacDonald, 2008).

Figure 6.1. Visual differences between adult male and female *R. avunculus*

6.3. Results

6.3.1. Overall

Adult male and female *R. avunculus* were significantly different during positional maintenance activities ($G = 59.966$, $p < 0.0001$). There were no significant differences between males and females during traveling ($G = 0.237$, n.s.), resting ($G = 5.561$, n.s.) and displaying ($G = 0.569$, n.s.). There were significant differences between adult males and females during foraging ($G = 10.081$, $p < 0.05$), feeding ($G = 11.184$, $p < 0.05$) and social behaviors ($G = 28.381$, $p < 0.001$). Females more frequently foraged, fed and participated in social behaviors than males (Table 6.1; Figure 6.2).

There were significant differences in males and females in overall positional behaviors ($G = 23.979$, $p < 0.01$) and for stand ($G = 15.230$, $p < 0.01$). Specifically, adult males stood more frequently than adult females (Table 6.2; Figure 6.3).

Table 6.1. Maintenance activity budget of adult male and female *R. avunculus* in Khau Ca Forest

	Female		Male		
	n	%	n	%	
Travel	754	44.56%	833	45.90%	n.s.
Forage	54	3.19%	28	1.54%	*
Rest	661	39.07%	821	45.23%	n.s.
Feed	118	6.97%	77	4.24%	*
Display	41	2.42%	37	2.04%	n.s.
Social behaviors	64	3.78%	19	1.05%	***
Total	*1,692*	*100.00%*	*1,815*	*100.00%*	

Note. The last column represents significance of differences between frequencies of adult males and females during maintenance activities after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Overall males vs. females: $G = 59.966$, $p < 0.0001$.

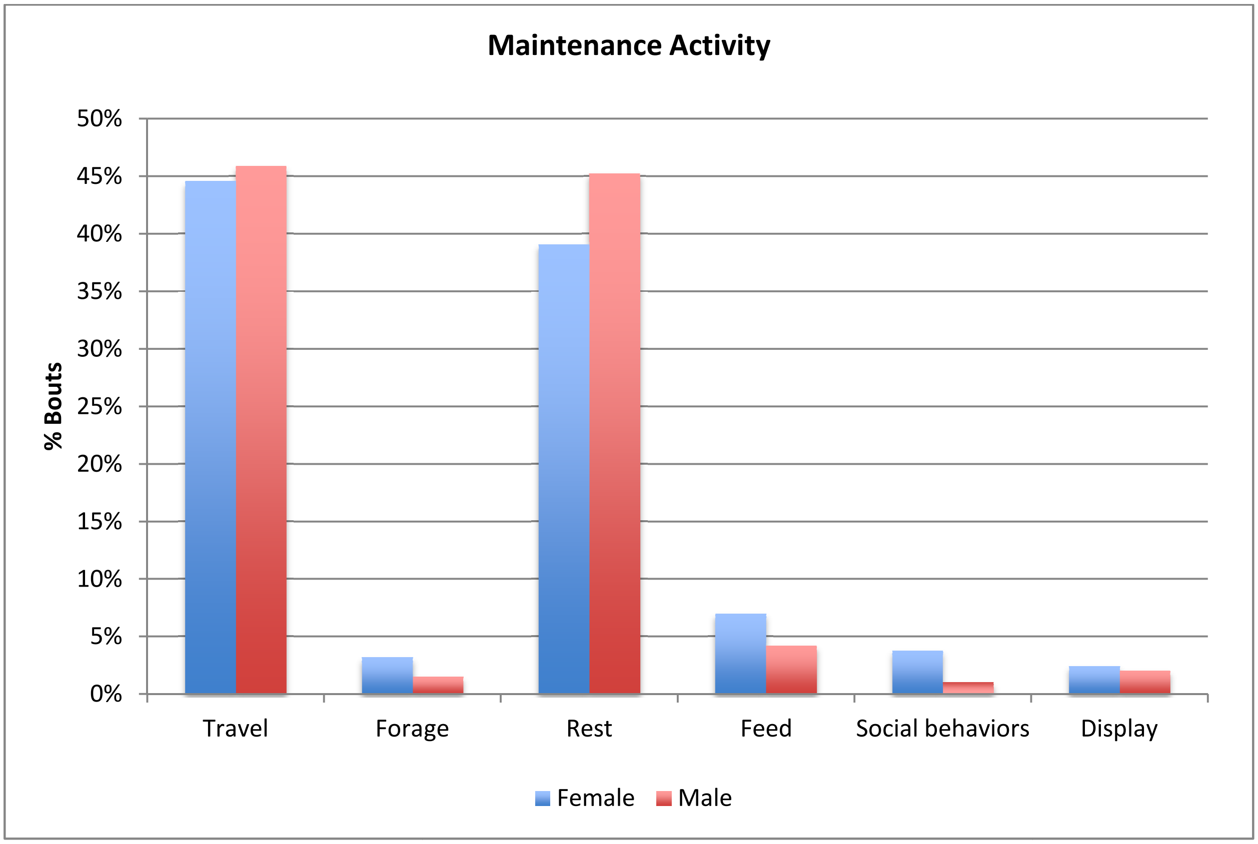

Figure 6.2. Maintenance activity budget of adult male and female *R. avunculus* in Khau Ca Forest

Table 6.2. Overall locomotor and postural profiles for adult male and adult female *R. avunculus* in Khau Ca Forest

	Female		Male		
	n	%	n	%	
Quadrupedalism	454	26.83%	459	25.29%	n.s.
Leap	105	6.21%	134	7.38%	n.s.
Climb	107	6.32%	114	6.28%	n.s.
Drop	80	4.73%	91	5.01%	n.s.
Arm-swing	50	2.96%	45	2.48%	n.s.
Other locomotion	12	0.71%	18	0.99%	n.s.
Sit	763	45.09%	774	42.64%	n.s.
Stand	66	3.90%	128	7.05%	**
Lie	18	1.06%	20	1.10%	n.s.
Cling	14	0.83%	17	0.94%	n.s.
Other posture	23	1.36%	15	0.83%	n.s.
Total	*1,692*	*100.00%*	*1,815*	*100.00%*	

Note. The last column represents significance of differences between frequencies of sexes and positional maintenance activities after comparisons using Bonferroni correction. n.s.: not significant, ** $p < 0.01$. Overall males and females: $G = 23.979$, $p < 0.01$.

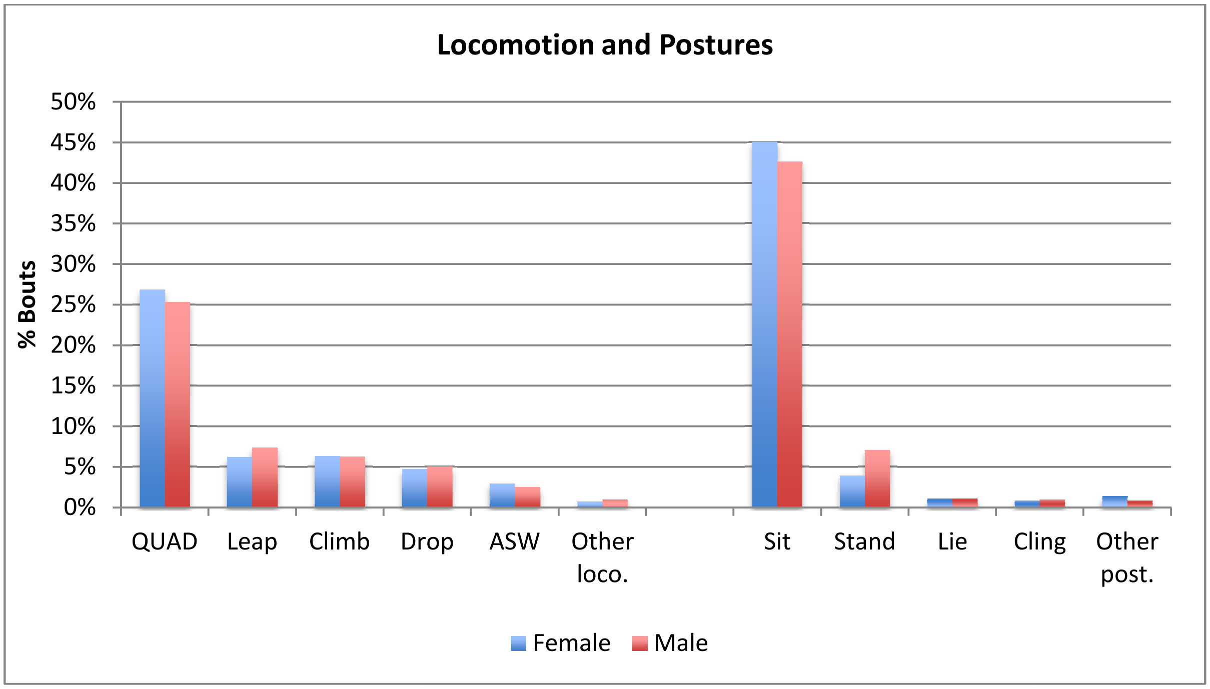

Figure 6.3. Frequencies of positional behaviors of adult male and female *R. avunculus* in Khau Ca Forest.

Note. QUAD: Quadrupedalism, ASW: Arm-swing, Other loco: Other locomotion includes bihop, bridge and bipedal walk, Other post.: Other postures include bipedal stand and fore-limb suspend (arm-hang).

6.3.2. Locomotion

There were no significant differences between the sexes in frequency of overall locomotion (G = 4.273, n.s.), and during travel (G = 3.531, n.s.) and foraging (G = 9.008, n.s.). The locomotion of both males and females was dominated by quadrupedalism (Females [F]: 56.19%; Males [M]: 53.31%), followed by leap (F: 13.00%; M: 15.56%), climb (F: 13.24%; M: 13.24%), drop (F: 9.90%; M: 10.57%), arm-swing (F: 6.19%; M: 5.23%) and other locomotion (F: 1.49%; M: 2.09%) (Table 6.3; Figure 6.4).

There were significantly different locomotor frequencies during travel and foraging for females (G = 18.959, p = 0.0001) but not for males (G = 3.164, p = 0.674). Adult females used leaping more frequently during travel and quadrupedalism more frequently during foraging. During travel, both males and females frequently used quadrupedalism (F: 54.77%; M: 52.70%), followed by leap (F: 13.93%; M: 15.85%), climb (F: 13.13%; M: 13.21%), drop (F: 10.48%; M: 10.68%), arm-swing (F: 6.37%; M: 5.40%) and other locomotion (F: 1.33%; M: 2.16%). During foraging, quadrupedalism (F: 75.93%; M: 71.43%) and climb (F: 14.81%; M: 14.29%) were the most commonly used locomotor modes for both males and females; although rarely observed, drop was reserved for males (7.14%), and arm-swing for females (3.70%) (Table 6.3).

6.3.3. Locomotion and Support Use

Adult males and females differed significantly in the frequencies of support size (12.723, p = 0.013) during overall locomotion, and support flexibility during overall locomotion (G = 5.251, p = 0.022) and by travel (G = 6.117, p = 0.013); there were no significant differences in use of support number and orientation during overall locomotion, and during travel and foraging for adult males and adult females. There was, however, a significant difference between adult males and adult females in use of support size during quadrupedal locomotion (Tables 6.4–6).

Both adult males and females used similar supports during overall locomotion, travel and foraging, and by locomotor modes. Single supports were used most frequently, followed by combined, multi, and network supports (Tables 6.4–6; Figure 6.5).

Table 6.3. Locomotor profiles for adult male and female *R. avunculus* in Khau Ca Forest

	Forage				Travel				Overall			
	Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%
Quadrupedalism	41	75.93%	20	71.43%	413	54.77%	439	52.70%	454	56.19%	459	53.31%
Leap	-	-	2	7.14%	105	13.93%	132	15.85%	105	13.00%	134	15.56%
Climb	8	14.81%	4	14.29%	99	13.13%	110	13.21%	107	13.24%	114	13.24%
Drop	1	1.85%	2	7.14%	79	10.48%	89	10.68%	80	9.90%	91	10.57%
Arm-swing	2	3.70%	-	-	48	6.37%	45	5.40%	50	6.19%	45	5.23%
Other	2	3.70%	-	-	10	1.33%	18	2.16%	12	1.49%	18	2.09%
Total	*54*	*100.00%*	*28*	*100.00%*	*754*	*100.00%*	*833*	*100.00%*	*808*	*100.00%*	*861*	*100.00%*

Note. n.s.: not significant, ** $p < 0.01$. Females vs. males: G(overall) = 4.273, n.s., G(forage) = 9.008, n.s., G(travel) = 3.531, n.s. Travel vs. Forage: G(female) = 18.959 **, G(male) = 3.164, n.s.

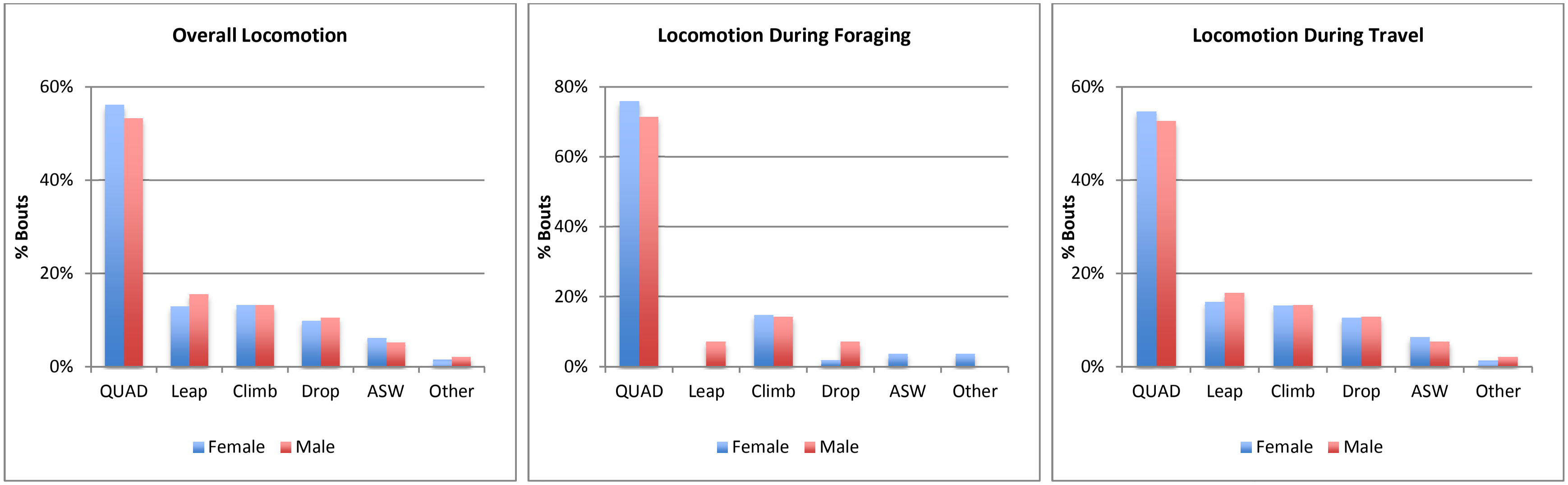

Figure 6.4. Frequencies of locomotor bouts during travel, foraging and overall by adult male and female *R. avunculus* in Khau Ca Forest.

Note. QUAD: Quadrupedalism, ASW: Arm-swing, Other: Other locomotion includes bihop, bipedal walk, bridge and unknown.

There were significant differences between adult males and females in use of support size ($G = 12.723$, $p < 0.05$) during overall locomotion. Males used trunks (2.79%) and branches (73.52) slightly more than females (1.98% for trunks and 70.30% for branches); while females used boughs (18.19%), twigs (7.80%) and lianas (1.73%) slightly more frequently than males. Specifically, there were no significant differences for males and females in use of support size during travel ($G = 4.440$, n.s.) and foraging ($G = 8.423$, n.s.). Only while quadrupedalism were there significant differences between adult males and females in use of support size; males used branches and trunks more often than females, while females used boughs, twigs and lianas more frequently than males (Tables 6.4–6; Figure 6.5).

There were no significant differences for adult males and females in use of support orientation in overall locomotion, during travel and foraging, and by each locomotor mode. Both adult males and female used horizontal supports, followed by oblique, vertical and terminal and forked supports (Tables 6.4–6; Figure 6.5).

There were significant differences between adult males and females in use of support flexibility in overall locomotion and during travel. Females used stable supports more frequent than males. This might be explained by adult females choosing stable supports while carrying their offspring during overall locomotion and during travel. Both males and females more frequently used flexible supports during foraging because their foods were primarily distributed in the periphery of the tree canopy (Tables 6.4–6; Figure 6.5).

Table 6.4. Locomotor maintenance activities and support use of adult male and female *R. avunculus* in Khau Ca Forest

	Forage				Travel				Total			
	Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%
Support number:												
Single	24	44.44%	12	42.86%	610	80.90%	645	77.43%	634	78.47%	657	76.31%
Combined	22	40.74%	10	35.71%	105	13.93%	141	16.93%	127	15.72%	151	17.54%
Multi	5	9.26%	4	14.29%	32	4.24%	35	4.20%	37	4.58%	39	4.53%
Network	3	5.56%	2	7.14%	7	0.93%	12	1.44%	10	1.24%	14	1.63%
Subtotal	*54*	*100.00%*	*28*	*100.00%*	*754*	*100.00%*	*833*	*100.00%*	*808*	*100.00%*	*861*	*100.00%*
Support size:												
Trunk	-	-	1	3.57%	16	2.12%	23	2.76%	16	1.98%	24	2.79%
Bough	1	1.85%	2	7.14%	146	19.36%	149	17.89%	147	18.19%	151	17.54%
Branch	35	64.81%	18	64.29%	533	70.69%	615	73.83%	568	70.30%	633	73.52%
Twig	13	24.07%	6	21.43%	50	6.63%	44	5.28%	63	7.80%	50	5.81%
Liana	5	9.26%	1	3.57%	9	1.19%	2	0.24%	14	1.73%	3	0.35%
Subtotal	*54*	*100.00%*	*28*	*100.00%*	*754*	*100.00%*	*833*	*100.00%*	*808*	*100.00%*	*861*	*100.00%*
Support orientation:												
Horizontal	35	64.81%	11	39.29%	314	41.64%	378	45.38%	349	43.19%	389	45.18%
Oblique	8	14.81%	10	35.71%	308	40.85%	319	38.30%	316	39.11%	329	38.21%
Vertical	5	9.26%	2	7.14%	83	11.01%	90	10.80%	88	10.89%	92	10.69%
Terminal	5	9.26%	5	17.86%	30	3.98%	33	3.96%	35	4.33%	38	4.41%
Fork	1	1.85%	-	-	19	2.52%	13	1.56%	20	2.48%	13	1.51%
Subtotal	*54*	*100.00%*	*28*	*100.00%*	*754*	*100.00%*	*833*	*100.00%*	*808*	*100.00%*	*861*	*100.00%*
Support flexibility:												
Flexible	39	72.22%	24	85.71%	353	46.82%	442	53.06%	392	48.51%	466	54.12%
Stable	15	27.78%	4	14.29%	401	53.18%	391	46.94%	416	51.49%	395	45.88%
Subtotal	*54*	*100.00%*	*28*	*100.00%*	*754*	*100.00%*	*833*	*100.00%*	*808*	*100.00%*	*861*	*100.00%*

Table 6.5. Locomotion and support use by adult male and female *R. avunculus* in Khau Ca Forest

	Quadrupedalism				Leap				Climb			
	Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%
<u>Support number:</u>												
Single	370	81.50%	375	81.70%	81	77.14%	101	75.37%	86	80.37%	82	71.93%
Combined	61	13.44%	69	15.03%	21	20.00%	28	20.90%	11	10.28%	12	10.53%
Multi	17	3.74%	7	1.53%	3	2.86%	3	2.24%	9	8.41%	17	14.91%
Network	6	1.32%	8	1.74%	-	-	2	1.49%	1	0.93%	3	2.63%
Subtotal	*454*	*100.00%*	*459*	*100.00%*	*105*	*100.00%*	*134*	*100.00%*	*107*	*100.00%*	*114*	*100.00%*
<u>Support size:</u>												
Trunk	1	0.22%	6	1.31%	1	0.95%	1	0.75%	12	11.21%	14	12.28%
Bough	117	25.77%	112	24.40%	13	12.38%	24	17.91%	11	10.28%	8	7.02%
Branch	310	68.28%	326	71.02%	80	76.19%	99	73.88%	71	66.36%	84	73.68%
Twig	23	5.07%	15	3.27%	11	10.48%	10	7.46%	3	2.80%	5	4.39%
Liana	3	0.66%	-	-	-	-	-	-	10	9.35%	3	2.63%
Subtotal	*454*	*100.00%*	*459*	*100.00%*	*105*	*100.00%*	*134*	*100.00%*	*107*	*100.00%*	*114*	*100.00%*
<u>Support orientation:</u>												
Horizontal	225	49.56%	232	50.54%	43	40.95%	65	48.51%	10	9.35%	15	13.16%
Oblique	215	47.36%	215	46.84%	42	40.00%	43	32.09%	19	17.76%	22	19.30%
Vertical	-	-	-	-	7	6.67%	11	8.21%	70	65.42%	71	62.28%
Terminal	10	2.20%	10	2.18%	6	5.71%	10	7.46%	2	1.87%	3	2.63%
Fork	4	0.88%	2	0.44%	7	6.67%	5	3.73%	6	5.61%	3	2.63%
Subtotal	*454*	*100.00%*	*459*	*100.00%*	*105*	*100.00%*	*134*	*100.00%*	*107*	*100.00%*	*114*	*100.00%*
<u>Support flexibility:</u>												
Flexible	192	42.29%	220	47.93%	56	53.33%	74	55.22%	45	42.06%	60	52.63%
Stable	262	57.71%	239	52.07%	49	46.67%	60	44.78%	62	57.94%	54	47.37%
Subtotal	*454*	*100.00%*	*459*	*100.00%*	*105*	*100.00%*	*134*	*100.00%*	*107*	*100.00%*	*114*	*100.00%*

Table 6.5 (continued)

	Drop				Arm-swing				Other locomotion			
	Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%
Support number:												
Single	53	66.25%	51	56.04%	34	68.00%	35	77.78%	10	83.33%	13	72.22%
Combined	19	23.75%	29	31.87%	13	26.00%	8	17.78%	2	16.67%	5	27.78%
Multi	6	7.50%	10	10.99%	2	4.00%	2	4.44%	-	-	-	-
Network	2	2.50%	1	1.10%	1	2.00%	-	-	-	-	-	-
Subtotal	*80*	*100.00%*	*91*	*100.00%*	*50*	*100.00%*	*45*	*100.00%*	*12*	*100.00%*	*18*	*100.00%*
Support size:												
Trunk	1	1.25%	2	2.20%	1	2.00%	1	2.22%	-	-	-	-
Bough	2	2.50%	2	2.20%	1	2.00%	3	6.67%	3	25.00%	2	11.11%
Branch	60	75.00%	75	82.42%	39	78.00%	35	77.78%	8	66.67%	14	77.78%
Twig	16	20.00%	12	13.19%	9	18.00%	6	13.33%	1	8.33%	2	11.11%
Liana	1	1.25%	-	-	-	-	-	-	-	-	-	-
Subtotal	*80*	*100.00%*	*91*	*100.00%*	*50*	*100.00%*	*45*	*100.00%*	*12*	*100.00%*	*18*	*100.00%*
Support orientation:												
Horizontal	37	46.25%	45	49.45%	26	52.00%	24	53.33%	8	66.67%	8	44.44%
Oblique	25	31.25%	27	29.67%	12	24.00%	15	33.33%	3	25.00%	7	38.89%
Vertical	6	7.50%	7	7.69%	5	10.00%	3	6.67%	-	-	-	-
Terminal	10	12.50%	9	9.89%	6	12.00%	3	6.67%	1	8.33%	3	16.67%
Fork	2	2.50%	3	3.30%	1	2.00%	-	-	-	-	-	-
Subtotal	*80*	*100.00%*	*91*	*100.00%*	*50*	*100.00%*	*45*	*100.00%*	*12*	*100.00%*	*18*	*100.00%*
Support flexibility:												
Flexible	61	76.25%	70	76.92%	34	68.00%	31	68.89%	4	33.33%	11	61.11%
Stable	19	23.75%	21	23.08%	16	32.00%	14	31.11%	8	66.67%	7	38.89%
Subtotal	*80*	*100.00%*	*91*	*100.00%*	*50*	*100.00%*	*45*	*100.00%*	*12*	*100.00%*	*18*	*100.00%*

Table 6.6. G-tests of independence in support use, maintenance activities, and locomotor behaviors by adult male and female *R. avunculus* in Khau Ca Forest

Males vs. Females	Support number	Support size	Support orientation	Support flexibility
Overall locomotion	1.523, n.s.	12.723 *	3.763, n.s.	5.251 *
Forage	0.614, n.s.	4.440, n.s.	7.712, n.s.	2.001, n.s.
Travel	3.795, n.s.	8.423, n.s.	3.714, n.s.	6.177 *
Quadrupedalism	5.082, n.s.	10.303 *	0.759, n.s.	2.933, n.s.
Leap	2.451, n.s.	1.861, n.s.	3.239, n.s.	0.085, n.s.
Climb	3.465, n.s.	5.981, n.s.	2.233, n.s.	2.481, n.s.
Drop	2.78, n.s.	3.262, n.s.	0.482, n.s.	0.011, n.s.
Arm-swing	2.339, n.s.	1.604, n.s.	3.062, n.s.	0.009, n.s.
Other locomotion	0.513, n.s.	0.990, n.s.	1.484, n.s.	2.256, n.s.

Note. n.s.: not significant, * $p < 0.05$.

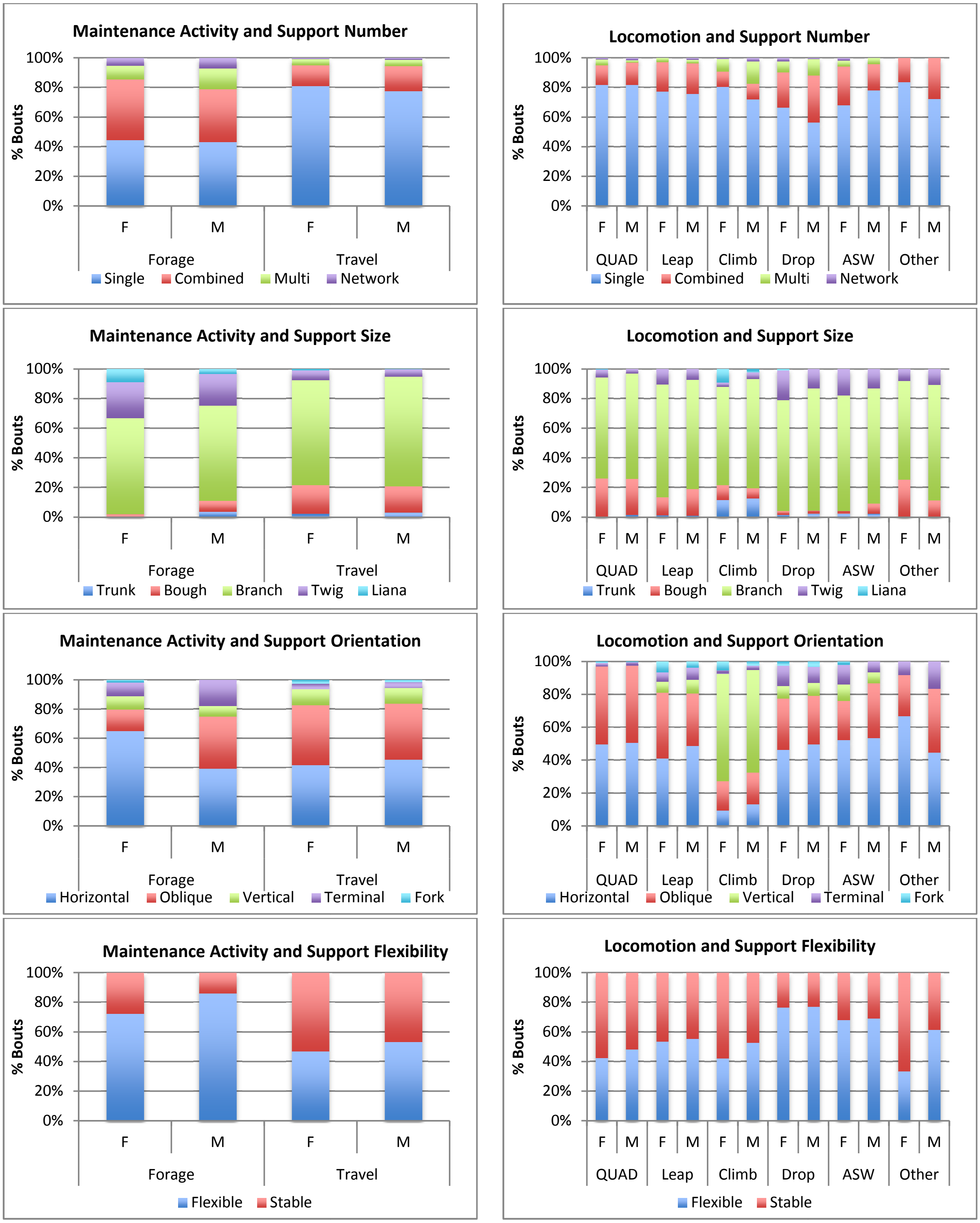

Figure 6.5. Frequencies of locomotion and support use by adult male and female *R. avunculus* in Khau Ca Forest

Note. QUAD: Quadrupedalism, ASW: Arm-swing, Other: Other locomotion includes bihop, bipedal walk, bridge and unknown.

6.3.4. Postures

There were only significant differences between sexes in overall postural behaviors ($G = 19.671$, $p < 0.001$), during rest ($G = 14.515$, $p < 0.01$) and social behavior ($G = 21.714$, $p < 0.001$), but no significant difference during feeding ($G = 6.182$, n.s.), displaying ($G = 7.444$, n.s.), or standing ($G = 14.252$, $p < 0.001$). The postures of both adult males and females were dominated by sit (F: 86.31%; M: 81.13%), followed by stand (F: 7.47%; M: 13.42%), lie (F: 2.04%; M: 2.10%), cling (F: 1.58%; M: 1.78%) and other postures (F: 2.60%; M: 1.57%). There were only significant sex-based differences in stand ($G = 10.419$, $p < 05$) during resting, and lie ($G = 13.555$, $p < 001$) and during social behavior (Tables 6.7–9; Figure 6.6).

Sit was most frequent posture overall and was also the most common posture during maintenance activities of adult male and female *R. avunculus*. Females sat more often than males during resting, displaying, and social behaviors while males sat more often than females during feeding (Table 6.8). There were significant differences for males and females in standing (F: 7.56%; M: 13.28%) during resting, and lying (F: 1.56%; M: 36.84%) during social behaviors. Lie did not occur during feeding while cling did not occur during social behaviors (Tables 6.8–9).

Table 6.7. Postural profiles of adult male and female *R. avunculus* in Khau Ca Forest

	Female		Male		
	n	%	n	%	
Sit	763	86.31%	774	81.13%	n.s.
Stand	66	7.47%	128	13.42%	***
Lie	18	2.04%	20	2.10%	n.s.
Cling	14	1.58%	17	1.78%	n.s.
Other	23	2.60%	15	1.57%	n.s.
Total	*884*	*100.00%*	*954*	*100.00%*	

Note. The last column represents significance of male and female differences in postural modes after comparisons using Bonferroni correction. n.s.: not significant, *** $p < 0.001$. Males vs. Femals: G = 19.671 ***.

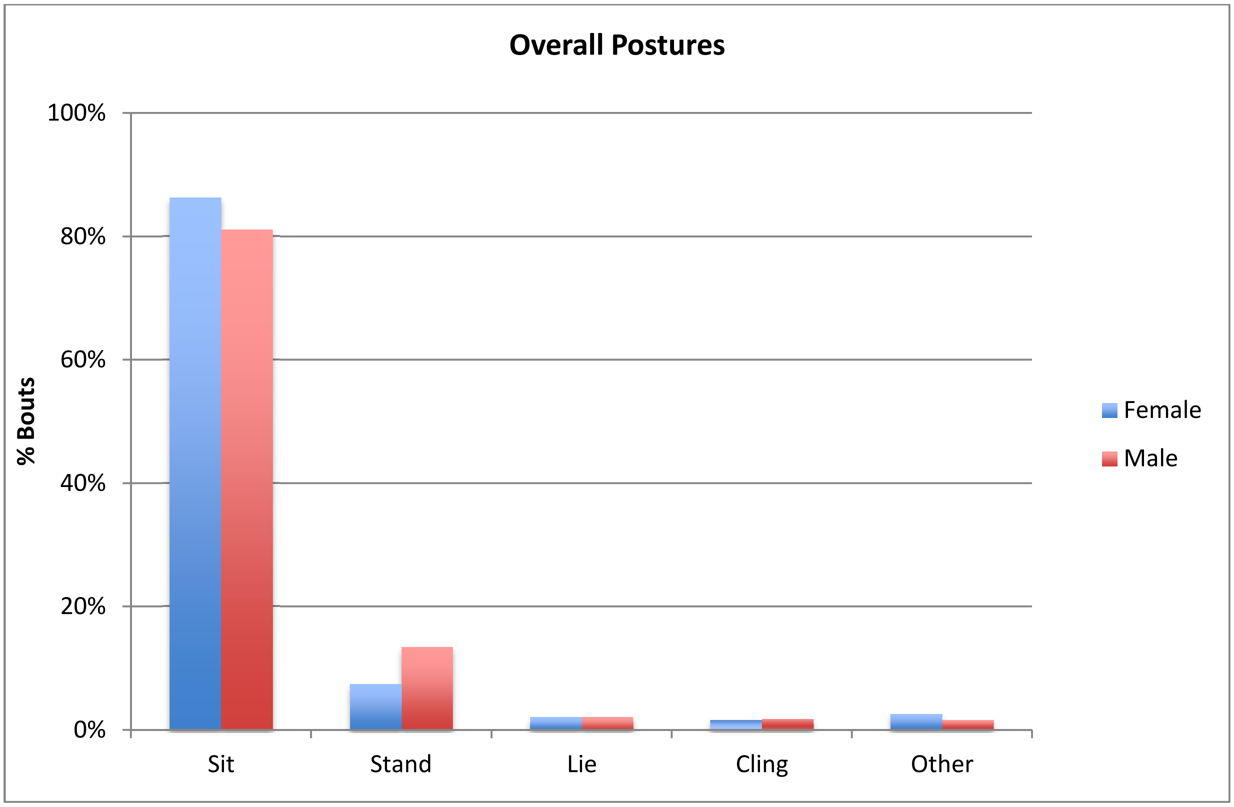

Figure 6.6. Frequencies of postural behaviors of adult male and female *R. avunculus* in Khau Ca Forest

Table 6.8. Postural profiles during resting, feeding, displaying and social behaviors for male and female *R. avunculus* in Khau Ca Forest

	Rest				Feed				Display				Social behaviors			
	Female		Male		Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Sit	575	86.99%	675	82.22%	104	88.14%	72	93.51%	23	56.10%	16	43.24%	61	95.31%	11	57.89%
Stand	50	7.56%	109	13.28%	2	1.69%	-	-	14	34.15%	18	48.65%	-	-	1	5.26%
Lie	15	2.27%	12	1.46%	-	-	-	-	2	4.88%	1	2.70%	1	1.56%	7	36.84%
Cling	10	1.51%	15	1.83%	4	3.39%	-	-	-	-	2	5.41%	-	-	-	-
Other	11	1.66%	10	1.22%	8	6.78%	5	6.49%	2	4.88%	-	-	2	3.13%	-	-
Total	*661*	*100.00%*	*821*	*100.00%*	*118*	*100.00%*	*77*	*100.00%*	*41*	*100.00%*	*37*	*100.00%*	*64*	*100.00%*	*19*	*100.00%*

Note. n.s.: not significant, ** $p < 0.01$. Females vs. males: G(rest) = 14.515 **, G(feed) = 6.182, n.s., G(display) = 7.444, n.s, G(social behaviors) = 21.714, $p < 0.001$.

Table 6.9. G-tests of independence in maintenance activities by postural modes of adult male and female *R. avunculus* in Khau Ca Forest

Males vs. Females	Rest	Feed	Display	Social behaviors
Overall postures	14.515 **	6.182 n.s.	7.444 n.s	21.714 ***
Sit	0.535, n.s.	0.078, n.s.	0.433, n.s.	1.450, n.s.
Stand	10.419 *	1.996, n.s.	0.707, n.s.	2.909, n.s.
Lie	1.277, n.s.	-	0.236, n.s.	13.555 ***
Cling	0.212, n.s.	3.966, n.s.	2.928, n.s.	-
Other posture	0.503, n.s.	0.005, n.s.	2.527, n.s.	1.026, n.s.

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

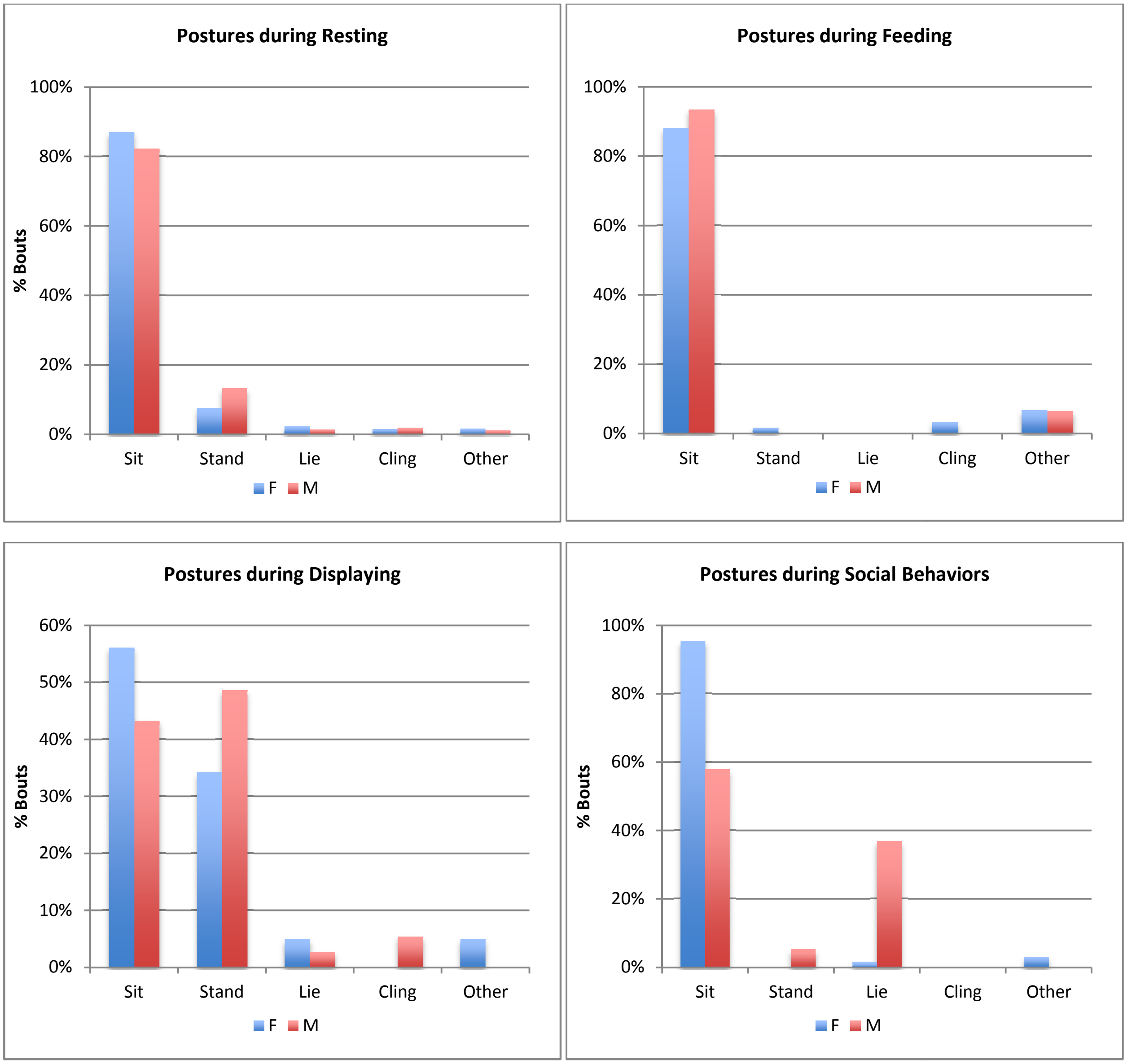

Figure 6.7. Frequencies of postural behaviors during resting, feeding, displaying and social behaviors by adult male and female *R. avunculus* in Khau Ca Forest.
Note. F: adult females, M: adult males.

6.3.5. Postures and Support Use

There were only significant differences between adult males and females in use of support size ($G = 14.125$, $p < 0.01$) during overall postures; there were no significant differences in use of support number ($G= 7.718$, n.s.), orientation ($G = 2.837$, n.s.) and flexibility ($G = 3.578$, n.s.) during overall postures.

Both adult males and females used single and combined supports most frequently, followed by multi and network supports during overall postures, maintenance activities, and by postural modes. There were significant differences for adult male and female *R. avunculus* in used of support number during resting ($G = 27.055$, $p < 0.001$), and while sitting ($G = 8.073$, $p < 0.05$) and lying ($G = 4.082$, $p < 0.05$). Males used combined supports more frequently than females while females used single supports more often than males (Tables 6.10–12; Figure 6.8).

Significant differences for adult males and females were seen in use of support size ($G = 14.125$, $p < 0.01$) overall postures, during resting ($G = 9.863$, $p < 0.05$) and feeding ($G = 11.292$, $p < 0.05$, and while sitting ($G = 12.545$, $p < 0.05$), standing ($G = 9.804$, $p < 0.05$), lying ($G = 5.492$, $p < 0.05$) and clinging ($G = 9.483$, $p < 0.05$). Branches and boughs were used most frequently by both adult males and females. Male used boughs more often than females during resting and feeding, and while sitting. Females sat on boughs more frequently than males while displaying and social behaviors. Males used branches slightly more frequently than females during all activities and postures, with the exception of lying; but these were not significantly different (Tables 6.10–12; Figure 6.8).

There were only significant differences for adult males and females in use of support orientation during displaying ($G = 9.987$, $p < 0.05$), while standing ($G = 13.555$, $p < 0.01$) and other postures ($G = 10.591$, $p < 0.05$). Horizontal and oblique supports were used most frequently by both adult males and females during all activities, and by postures. During resting, feeding and social behaviors, females used horizontal supports more often than males; in contrast they used these supports less while displaying. Females used oblique supports more frequently than males during resting and displaying, and less during feeding and social behaviors (Table 6.10). Males used horizontal supports more frequently than females when standing, lying and clinging, and less when sitting and other postures. Females used oblique supports more frequent than males when standing only. Forked, terminal and vertical supports were seldom used. Overall, females used terminal and vertical supports more frequent than males while males used forked supports more frequent than females (Tables 6.10–12; Figure 6.8).

Overall, stable supports were used slightly more frequently by both males and females. Statistically, there were only significant differences for males and females in use support flexibility during displaying ($G = 7.357$, $p < 0.01$), while standing ($G = 4.088$, $p < 0.05$), and other postures ($G = 14.660$, $p < 0.001$). During resting, feeding and displaying, males used flexible supports more frequently and stable supports less than females. During social behaviors, females used flexible supports more frequently and stable supports less than males. Females also used stable supports more frequently than males with all postures, except lying (Tables 6.10–12; Figure 6.8).

Table 6.10. Postural maintenance activities and support use of male and female *R. avunculus* in Khau Ca Forest

	Rest				Feed				Display				Social behaviors			
	Female		Male		Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Support number:																
Single	631	95.46%	726	88.43%	66	55.93%	44	57.14%	39	95.12%	32	86.49%	56	87.50%	18	94.74%
Combined	22	3.33%	78	9.50%	32	27.12%	16	20.78%	2	4.88%	5	13.51%	6	9.38%	1	5.26%
Multi	6	0.91%	9	1.10%	11	9.32%	10	12.99%	-	-	-	-	1	1.56%	-	-
Network	2	0.30%	8	0.97%	9	7.63%	7	9.09%	-	-	-	-	1	1.56%	-	-
Subtotal	*661*	*100.00%*	*821*	*100.00%*	*118*	*100.00%*	*77*	*100.00%*	*41*	*100.00%*	*37*	*100.00%*	*64*	*100.00%*	*19*	*100.00%*
Support size:																
Trunk	9	1.36%	4	0.49%	2	1.69%	5	6.49%	-	-	1	2.70%	1	1.56%	-	-
Bough	140	21.18%	184	22.41%	4	3.39%	9	11.69%	12	29.27%	8	21.62%	20	31.25%	3	15.79%
Branch	498	75.34%	616	75.03%	71	60.17%	47	61.04%	27	65.85%	27	72.97%	41	64.06%	16	84.21%
Twig	8	1.21%	16	1.95%	33	27.97%	14	18.18%	2	4.88%	1	2.70%	1	1.56%	-	-
Liana	6	0.91%	1	0.12%	8	6.78%	2	2.60%	-	-		0.00%	1	1.56%	-	-
Subtotal	*661*	*100.00%*	*821*	*100.00%*	*118*	*100.00%*	*77*	*100.00%*	*41*	*100.00%*	*37*	*100.00%*	*64*	*100.00%*	*19*	*100.00%*
Support orientation:																
Horizontal	369	55.82%	464	56.52%	62	52.54%	39	50.65%	13	31.71%	18	48.65%	43	67.19%	8	42.11%
Oblique	239	36.16%	290	35.32%	26	22.03%	24	31.17%	26	63.41%	12	32.43%	20	31.25%	9	47.37%
Vertical	16	2.42%	17	2.07%	5	4.24%		0.00%	-	-	1	2.70%	-	-	-	-
Terminal	4	0.61%	9	1.10%	21	17.80%	9	11.69%	-	-	1	2.70%	-	-	-	-
Fork	33	4.99%	41	4.99%	4	3.39%	5	6.49%	2	4.88%	5	13.51%	1	1.56%	2	10.53%
Subtotal	*661*	*100.00%*	*821*	*100.00%*	*118*	*100.00%*	*77*	*100.00%*	*41*	*100.00%*	*37*	*100.00%*	*64*	*100.00%*	*19*	*100.00%*
Support flexibility:																
Flexible	212	32.07%	319	38.86%	92	77.97%	65	84.42%	15	36.59%	19	51.35%	18	28.13%	2	10.53%
Stable	449	67.93%	502	61.14%	26	22.03%	12	15.58%	26	63.41%	18	48.65%	46	71.88%	17	89.47%
Subtotal	*661*	*100.00%*	*821*	*100.00%*	*118*	*100.00%*	*77*	*100.00%*	*41*	*100.00%*	*37*	*100.00%*	*64*	*100.00%*	*19*	*100.00%*

Table 6.11. Percentages of postural bouts and support use by male and female *R. avunculus* in Khau Ca Forest

	Sit				Stand				Lie			
	Female		Male		Female		Male		Female		Male	
	n	%	n	%	n	%	n	%	n	%	n	%
Support number:												
Single	681	89.25%	665	85.92%	58	87.88%	113	88.28%	18	100.00%	17	85.00%
Combined	53	6.95%	85	10.98%	7	10.61%	9	7.03%	-	-	3	15.00%
Multi	17	2.23%	14	1.81%	1	1.52%	3	2.34%	-	-	-	-
Network	12	1.57%	10	1.29%	-	-	3	2.34%	-	-	-	-
Subtotal	*763*	*100.00%*	*774*	*100.00%*	*66*	*100.00%*	*128*	*100.00%*	*18*	*100.00%*	*20*	*100.00%*
Support size:												
Trunk	9	1.18%	7	0.90%	-	-	1	0.78%	-	-	-	-
Bough	146	19.13%	172	22.22%	24	36.36%	24	18.75%	1	5.56%	7	35.00%
Branch	560	73.39%	570	73.64%	37	56.06%	96	75.00%	17	94.44%	13	65.00%
Twig	37	4.85%	23	2.97%	5	7.58%	6	4.69%	-	-	-	-
Liana	11	1.44%	2	0.26%	-	-	1	0.78%	-	-	-	-
Subtotal	*763*	*100.00%*	*774*	*100.00%*	*66*	*100.00%*	*128*	*100.00%*	*18*	*100.00%*	*20*	*100.00%*
Support orientation:												
Horizontal	438	57.40%	428	55.30%	29	43.94%	83	64.84%	7	38.89%	11	55.00%
Oblique	268	35.12%	282	36.43%	26	39.39%	36	28.13%	8	44.44%	9	45.00%
Vertical	-	-	-	-	5	7.58%	4	3.13%	3	16.67%	-	-
Terminal	22	2.88%	15	1.94%	1	1.52%	4	3.13%	-	-	-	-
Fork	35	4.59%	49	6.33%	5	7.58%	1	0.78%	-	-	-	-
Subtotal	*763*	*100.00%*	*774*	*100.00%*	*66*	*100.00%*	*128*	*100.00%*	*18*	*100.00%*	*20*	*100.00%*
Support flexibility:												
Flexible	291	38.14%	309	39.92%	25	37.88%	68	53.13%	7	38.89%	3	15.00%
Stable	472	61.86%	465	60.08%	41	62.12%	60	46.88%	11	61.11%	17	85.00%
Subtotal	*763*	*100.00%*	*774*	*100.00%*	*66*	*100.00%*	*128*	*100.00%*	*18*	*100.00%*	*20*	*100.00%*

Table 6.11 (continued)

	Cling				Other posture			
	Female		Male		Female		Male	
	n	%	n	%	n	%	n	%
Support number:								
Single	14	100.00%	14	82.35%	21	91.30%	11	73.33%
Combined	-	-	2	11.76%	2	8.70%	1	6.67%
Multi	-	-	1	5.88%	-	-	1	6.67%
Network	-	-	-	-	-	-	2	13.33%
Subtotal	*14*	*100.00%*	*17*	*100.00%*	*23*	*100.00%*	*15*	*100.00%*
Support size:								
Trunk	3	21.43%	2	11.76%		0.00%	-	-
Bough	1	7.14%	1	5.88%	4	17.39%	-	-
Branch	6	42.86%	13	76.47%	17	73.91%	14	93.33%
Twig	-	-	1	5.88%	2	8.70%	1	6.67%
Liana	4	28.57%	-	-	-	-	-	-
Subtotal	*14*	*100.00%*	*17*	*100.00%*	*23*	*100.00%*	*15*	*100.00%*
Support orientation:								
Horizontal		0.00%	2	11.76%	13	56.52%	5	33.33%
Oblique	1	7.14%	2	11.76%	8	34.78%	6	40.00%
Vertical	13	92.86%	12	70.59%		0.00%	2	13.33%
Terminal	-	-	-	-	2	8.70%	-	-
Fork	-	-	1	5.88%	-	-	2	13.33%
Subtotal	*14*	*100.00%*	*17*	*100.00%*	*23*	*100.00%*	*15*	*100.00%*
Support flexibility:								
Flexible	6	42.86%	11	64.71%	8	34.78%	14	93.33%
Stable	8	57.14%	6	35.29%	15	65.22%	1	6.67%
Subtotal	*14*	*100.00%*	*17*	*100.00%*	*23*	*100.00%*	*15*	*100.00%*

Table 6.12. G-tests of independence in support use, maintenance activities, and postural behaviors by adult male and female *R. avunculus* in Khau Ca Forest

Males vs. Females	Support number	Support size	Support orientation	Support flexibility
Overall	7.718, n.s.	14.125 **	2.837, n.s.	3.578, n.s.
Rest	27.055 ***	9.863 *	1.345, n.s.	7.357 **
Feed	1.480, n.s.	11.292 *	8.658, n.s.	1.263, n.s.
Display	1.814, n.s.	2.326, n.s.	9.987 *	1.729, n.s.
Social behaviors	1.451, n.s.	3.818, n.s.	5.247, n.s.	2.828, n.s.
Sit	8.073 *	12.545 *	4.070, n.s.	0.514, n.s.
Stand	3.289, n.s.	9.804 *	13.555 **	4.088 *
Lie	4.082 *	5.492 *	5.009, n.s.	2.836, n.s.
Cling	3.868, n.s.	9.483 *	4.248, n.s.	1.488, n.s.
Other posture	5.980, n.s.	4.479, n.s.	10.591 *	14.660 ***

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Figure 6.8. Frequencies of postures and support use by adult male and female *R. avunculus* in Khau Ca Forest

6.4. Discussion

A primary aim of this chapter was to ascertain sex-based differences in positional behavior and support use of *R. avunculus* based on body size effect hypothesis of Fleagle and Mittermeier (1980). The results of this study do not provide support for Hypothesis 6.1 as adult male and female *R. avunculus* were significantly different during maintenance activities, and by overall positional behaviors.

In Hypothesis 6.2 I predicted that, being larger-bodied, adult male *R. avunculus* would more frequently climb and suspend, and less frequently leap than the smaller-bodied adult females (following Fleagle and Mittermeier, 1980). However, my results indicated that there were no significant sexual differences in frequency of overall locomotion, and during travel and foraging as predicted by Hypothesis 6.1. Both adult male and female's locomotion were dominated by quadrupedalism, followed by leap, climb, drop, arm-swing and other locomotion. These findings are in agreement with the results of Gebo (1992), and Gebo and Chapman (1995b) (Table 6.13).

Although there were no differences in overall locomotion, and during travel and foraging, adult male and female *R. avunculus* significantly differed in use of support size and flexibility. But, the results do not support Hypothesis 6.3 that predicted larger adult males would use larger substrates more commonly than females. The results indicated that males used trunks and branches more than females while females used boughs, twigs and lianas more frequently than males. Females used stable supports more frequently than males, and males used flexible supports more frequently than females during overall locomotion, during travel and foraging, and by locomotor modes. In finer comparisons, adult females more often employed safer locomotor modes, i.e., more quadrupedal walk, and more frequently selected larger and stable supports during locomotor activities. These results were similar to previous results of Chatani (2003) and Fan *et al.* (2013) suggested that females are more likely to use less risky behaviors than males because of the need to take care of their offspring while moving on arboreal supports.

Table 6.13. Sex-based differences in locomotion of primates

	Body size (kg)	Activity	Quadupedalism	Leap	Climb	Drop	Suspensory	Other
Alouatta palliata[1]	M: 7.27	Overall	48.0%	5.0%	35.0%	-	2.0%	10.0%
	F: 5.52		45.0%	4.00%	38.0%	-	2.0%	11.0%
	M	Travel	49.0%	5.0%	33.0%	-	1.0%	12.0%
	F		50.0%	5.0%	33.0%	-	1.0%	11.0%
	M	Feeding	46.0%	4.0%	39.0%	-	4.0%	7.0%
	F		42.0%	3.0%	45.0%	-	2.0%	8.0%
Cebus capucinus[1]	M: 3.68	Overall	58.0%	17.0%	22.0%	-	< 1.0%	< 3.0%
	F: 2.54		49.0%	15.0%	29.0%	-	< 2.0%	< 7.0%
Cercopithecus ascanius[2]	M: 4.05	Travel	42.0%	26.0%	27.0%	-	-	5.0%
	F: 2.80		41.0%	24.0%	27.0%	-	-	8.0%
	M	Feeding	38.0%	12.0%	48.0%	-	-	2.0%
	F		38.0%	10.0%	50.0%	-	-	2.0%
Cercopithecus mitis[2]	M: 7.40	Travel	50.0%	18.0%	29.0%	-	< 1.0%	< 3.0%
	F: 3.83		51.0%	18.0%	29.0%	-	-	2.0%
	M	Feeding	55.0%	5.0%	39.0%	-	-	1.0%
	F		56.0%	6.0%	37.0%	-	-	1.0%
Cercopithecus albigena[2]	M: 8.75	Travel	46.0%	21.0%	33.0%	-	-	< 1.0%
	F: 6.36		46.0%	22.0%	31.0%	-	-	1.0%
	M	Feeding	44.0%	13.0%	42.0%	-	-	-
	F		51.0%	10.0%	38.0%	-	< 1.0%	< 1.0%
Colobus badius[2]	M: 8.39	Travel	35.0%	31.0%	29.0%	-	-	5.0%
	F: 7.84		33.0%	30.0%	29.0%	-	< 1.0%	< 8.0%
	M	Feeding	47.0%	14.0%	36.0%	-	< 1.0%	< 3.0%
	F		43.0%	18.0%	37.0%	-	< 1.0%	< 2.0%
Colobus guereza[2]	M: 9.53	Travel	39.0%	44.0%	11.0%	-	< 1.0%	< 6.0%
	F: 7.65		39.0%	45.0%	10.0%	-	-	6.0%
	M	Feeding	44.0%	30.0%	20.0%	-	-	6.0%
	F		44.0%	33.0%	19.0%	-	-	4.0%

Table 6.13 (continued)

	Body size* (kg)	Activity	Quadupedalism		Leap	Climb	Drop	Suspensory	Other
			Walk	Run					
Rhinopithecus avunculus[3]	M: 14.50	Overall	53.31%		15.56%	13.24%	10.57%	5.23%	2.09%
	F: 8.25		56.19%		13.00%	13.24%	9.90%	6.19%	1.49%
	M	Travel	52.70%		15.85%	13.21%	10.68%	5.40%	2.16%
	F		54.77%		13.93%	13.13%	10.48%	6.37%	1.33%
	M	Foraging	71.43%		7.14%	14.29%	7.14%	-	-
	F		75.93%		0.00%	14.81%	1.85%	3.70%	3.70%
Macaca fuscata[4]	M: 11.00	Ground travel	67.1%	26.6%	6.3%	-	-	-	-
	F: 8.00		49.4%	45.5%	4.6%	-	-	-	0.5%
	M	Ground feeding	98.6%	-	-	-	-	-	1.4%
	F		100.0%	-	-	-	-	-	-
		Arboreal travel							<
	M		90.8%	2.6%	6.6%	-	-	-	0.10%
	F		86.0%	0.6%	9.3%		4.0%	-	0.1%
	M	Arboreal feeding	50.0%	-	28.0%	13.3%	-	-	8.7%
	F		92.1%	-	6.0%	0.9%	-	-	1.0%
Trachypithecus delacouri[5]	M	Travel	65.0%		6.0%	28.0%	-	-	1.0%
	F		63.0%		9.0%	27.0%	-	-	1.0%
	M	Feed	77.0%		10.0%	12.0%	-	-	1.0%
	F		79.0%		8.0%	8.0%	-	-	5.0%
	M	Social behaviors	100.0%		-	-	-	-	-
	F		87.0%		-	-	-	-	13.0%
Nomascus nasutus[6]	M	Locomotion	0.5%	-	13.4%	17.3%	-	58.7%	10.1%
	F		1.4%	-	4.1%	25.2%	-	52.6%	16.7%

Table 6.13 (continued)

	Body size* (kg)	Activity	Quadupedalism	Leap	Climb	Drop	Suspensory	Other
Pan troglodytes[7]	M: 59.70	Overall locomotion	86.60%	-	11.1%	-	1.1%	1.2%
	F: 45.80		85.60%	0.6%	10.9%	-	1.4%	1.2%
	M	Travel	89.30%	0.2%	9.6%	-	0.8%	0.2%
	F		85.70%	0.2%	12.6%	-	1.5%	-
	M	Feeding	81.10%	-	9.0%	-	4.5%	5.4%
	F		85.50%	0.7%	5.3%	-	3.9%	4.6%
	M	Arboreal locomotion	11.70%	-	76.7%	-	5.8%	5.8%
	F		16.40%	1.6%	59.8%	-	7.40%	0.8%
Pongo pygmaeus abelii[8]	M: 78.50	Overall	46.0%	-	9.0%	-	21.0%	24.0%
	F: 35.80		61.8%	-	10.8%	-	18.0%	6.0%

Note. * Body size followed Fleagle (2013), M = Male, F = Female. [1] Gebo (1992), [2] Gebo and Chapman (1995b), [3] In this study, [4] Chatani (2003), [5] Workman and Schmitt (2012), [6] Fan *et al*. (2013), [7] Doran (1993), [8] Sugardjito and Vanhooff (1986).

Table 6.14. Sex-based differences in postures by primates

	Body size (kg)	Activity	Squat	Sit	Stand	Lie	Cling	Other
Alouatta palliata[1]	M: 7.27	Travel	-	55.00%	24.00%	16.00%	-	5.00%
	F: 5.52		-	53.00%	21.00%	19.00%	-	7.00%
	M	Feeding	-	53.00%	18.00%	9.00%	-	-
	F		-	52.00%	18.00%	8.00%	-	20.00%
	M	Overall	-	53.00%	21.00%	12.00%	-	14.00%
	F		-	52.00%	19.00%	12.00%	-	17.00%
Cebus capucinus[1]	M: 3.68	Overall	-	38.00%	37.00%	19.00%	-	6.00%
	F: 2.54		-	50.00%	26.00%	4.00%	-	20.00%
Rhinopithecus avunculus[2]	M: 14.50	Overall	-	81.13%	13.42%	2.10%	1.78%	1.57%
	F: 8.25		-	86.31%	7.47%	2.04%	1.58%	2.60%
	M	Rest	-	82.22%	13.28%	1.46%	1.83%	1.22%
	F		-	86.99%	7.56%	2.27%	1.51%	1.66%
	M	Feed	-	93.51%	6.49%	-	-	-
	F		-	88.14%	6.78%	-	-	3.39%
	M	Display	-	43.24%	48.65%	2.70%	5.41%	-
	F		-	56.10%	34.15%	4.88%	-	4.88%
	M	Social	-	57.89%	5.26%	36.84%	-	-
	F		-	95.31%	-	1.56%	-	3.13%
Macaca fuscata[3]	M: 11.00	Ground rest	-	19.30%	-	80.70%	-	-
	F: 8.00		-	34.10%	-	65.90%	-	-
	M	Ground feeding	-	9.60%	90.40%	-	-	-
	F		-	19.30%	79.60%	-	-	1.10%
	M	Arboreal rest	-	56.80%	3.30%	39.80%	-	0.10%
	F		-	96.00%	-	4.00%	-	0.10%
	M	Arboreal feeding	-	26.40%	53.20%	-	-	20.50%
	F		-	23.10%	51.30%	-	-	25.60%

Table 6.14 (continued)

	Body size (kg)	Acivity	Squat	Sit	Stand	Lie	Cling	Other
Pan troglodytes[4]	M: 59.70	Overall	-	70.80%	6.10%	22.10%	-	1.00%
	F: 45.80		-	80.60%	5.60%	11.60%	-	2.10%
	M	Feed	-	86.70%	9.30%	2.00%	-	2.00%
	F		-	-	-	-	-	-
	M	Rest	-	49.90%	0.40%	51.50%	-	-
	F		-	67.50%	1.00%	31.30%	-	1.00%
	M	Groom	-	84.10%	5.30%	10.10%	-	0.50%
	F		-	90.80%	3.10%	6.10%	-	-
Gorilla g. gorilla[5]	Lone male: 170.40	Overall	29.00%	44.00%	5.00%	16.00%	-	6.00%
	Group male		21.00%	66.00%	3.00%	6.00%	-	4.00%
	F: 71.50		37.00%	44.00%	5.00%	5.00%	-	9.00%
	Lone male	Feed	62.00%	36.00%	2.00%	-	-	< 1.00%
	Group male		28.00%	65.00%	2.00%	-	-	5.00%
	F		34.00%	53.00%	4.00%	1.00%	-	8.00%
	Lone male	Forage	20.00%	27.00%	-	-	-	53.00%
	Group male		-	50.00%	17.00%	-	-	33.00%
	F		81.00%	16.00%	-	-	-	3.00%
	Lone male	Rest	18.00%	49.00%	7.00%	22.00%	-	4.00%
	Group male		10.00%	69.00%	3.00%	15.00%	-	3.00%
	F		30.00%	47.00%	8.00%	5.00%	-	10.00%
Pongo pygmaeus abelii[6]	M: 78.50	Rest	-	80.0%	2.0%	15.0%	-	3.0%
	F: 35.80		-	46.3%	3.1%	46.5%	-	4.1%
	M	Pause	-	54.0%	33.0%	-	-	23.0%
	F		-	38.0%	25.8%	-	-	36.0%

Note. * Body size followed Fleagle (2013); M = Male, F = Female. [1] Gebo (1992), [2]In this study, [3]Chatani (2003), [4] Doran (1993), [5] Remis (1995), [6] Sugardjito and Vanhooff (1986).

Table 6.15. Sex-based differences in support size use by primates

	Body size (kg)	Activity	Ground	Trunk	Bough	Branch	Twigs	Other
Alouatta palliata[1]	M: 7.27	Overall	-	-	28.0%	45.0%	27.0%	-
	F: 5.52		-	-	20.0%	40.0%	40.0%	-
Cebus capucinus[1]	M: 3.68	Overall	-	-	13.0%	50.0%	37.0%	-
	F: 2.54		-	-	6.0%	36.0%	58.0%	-
Cercopithecus ascanius[2]	M: 4.05	Overall	-	-	12.0%	53.0%	35.0%	-
	F: 2.80		-	-	8.0%	51.0%	41.0%	-
Cercopithecus mitis[2]	M: 7.40	Overall	-	-	14.0%	63.0%	23.0%	-
	F: 3.83		-	-	13.0%	60.0%	28.0%	-
Cercopithecus albigena[2]	M: 8.75	Overall	-	-	17.0%	60.0%	23.0%	-
	F: 6.36		-	-	21.0%	53.0%	26.0%	-
Colobus badius[2]	M: 8.39	Overall	-	-	20.0%	67.0%	13.0%	-
	F: 7.84		-	-	9.0%	68.0%	22.0%	-
Colobus guereza[2]	M: 9.53	Overall	-	-	28.0%	58.0%	14.0%	-
	F: 7.65		-	-	20.0%	62.0%	17.0%	-
Rhinopithecus avunculus[3]	M: 14.50	Overall	-	1.87%	19.56%	73.77%	4.46%	0.33%
	F: 8.25		-	1.65%	19.09%	71.22%	6.32%	1.71%
	M	Locomotion	-	2.79%	17.54%	73.52%	5.81%	0.35%
	F		-	1.98%	18.19%	70.30%	7.80%	1.73%
	M	Posture	-	1.05%	21.38%	74.00%	3.25%	0.31%
	F		-	1.36%	19.91%	72.06%	4.98%	1.70%
Trachypithecus delacouri	M	Rest	-	98.0%	< 1.0%	1.0%	-	< 1.0%
	F		-	98.0%	< 1.0%	1.0%	-	< 1.0%
	M	Feed	-	95.0%	5.0%	-	-	< 1.0%
	F		-	91.0%	8.0%	-	-	< 1.0%
	M	Social behaviors	-	71.0%	22.0%	7.0%	-	-
	F		-	72.0%	21.0%	6.0%	-	< 1.0%

Table 6.15 (continued)

	Body size (kg)	Activity	Ground	Trunk	Bough	Branch	Twigs	Other
Nomascus nasutus[4]	M	Locomotion	-	-	3.5%	71.7%	18.7%	6.2%
	F		-	-	2.3%	67.0%	21.7%	8.9%
Pan troglodytes[5]	M: 59.70	Overall locomotion	85.8%	4.9%	1.4%	2.6%	2.6%	2.6%
	F: 45.80		82.2%	6.1%	1.3%	4.1%	1.9%	4.4%
	M	Travel	88.9%	5.3%	0.8%	0.8%	1.2%	3%
	F		84.2%	6.4%	0.7%	1.3%	1.9%	5.3%
	M	Feeding	77.1%	2.7%	3.7%	12.8%	3.7%	-
	F		74.5%	5.2%	3.3%	13.7%	2%	1.3%
	M	Arboreal locomotion	-	34.9%	9.7%	18.4%	18.4%	18.4%
	F		-	34.3%	7.4%	22.9%	10.7%	24.6%
	M	Overall postures	62.2%	8.6%	9.6%	18.3%	0.1%	1.2%
	F		39.6%	13.9%	13%	30.9%	0.4%	2.1%
	M	Arboreal posture	-	20.8%	25.6%	48.2%	-	5.3%
	F		-	19.7%	21%	51.1%	0.7%	7.4%
Gorilla g. gorilla[6]	Lone male: 170.40	Overall	-	4%	38%	18%	6%	34%
	Group male		-	4%	62%	8%	-	26%
	F: 71.50		-	5%	23%	37%	8%	27%

Note. * Body size followed Fleagle (2013); M = Male, F = Female. [1] Gebo (1992), [2] Gebo and Chapman (1995b), [3] In this study, [4] Fan *et al.* (2013), [5] Doran (1993), [6] Remis (1995).

Predictions of sex-based differences in postures and support use by *R. avunculus* were not supported by the results of this study. Hypothesis 6.2 predicted larger adult males would more frequently use sitting and standing behaviors, and less frequently bipedal stand and cling than females. Adult males and females significantly differed in overall postural behaviors, and during resting and social behaviors; but did not differ during feeding and displaying. Throughout this study, females used sitting more often than males during resting, displaying and social behaviors, but not during feeding. The frequency of standing by adult males and females supports Hypothesis 6.2. These *R. avunculus'* sex-based differences are similar to most of other primates (Table 6.14).

Adult male and female *R. avunculus* rarely used lying, clinging and other postures (including bipedal stand and suspensory posture) during overall postures and during postural maintenance activities. Although there were slight differences between adult males and females in the frequencies of lying, clinging and other postures, they failed to reach statistical significance. This result also does not provide support for Hypothesis 6.2.

Single and combined supports were most frequently used by both adult males and females during postural maintenance activities and by postural modes. Adult males and females significantly differed in the frequencies of used support number during resting, and while sitting and lying. There were no reports of sex-based differences in use of support number in the previous studies used for comparison.

Adult male and female *R. avunculus* differed significantly in frequencies of support size use. Both sexes preferred medium-sized branches and large-sized boughs during postural maintenance activities, and by postural modes that are similar to other large-sized primates. Hypothesis 6.3 is supported by results of support size use. However, when data are grouped into broader categories of overall activities, and overall locomotion and postures, adult male and female *R. avunculus* differed just slightly in the frequencies of support size use, about 2 – 3% of bout total, and are similar to adult males and females of similar-sized and smaller-sized primates including African cercopithecids, and New World monkeys in arboreal locomotion and postures.

Adult male and female Cao Vit gibbons (*Nomascus nasutus*) and western lowland gorillas (*Gorilla gorilla*) differ significantly in frequencies of support size; larger-bodied males used larger supports than did smaller-bodies females (Table 6.15).

Similar to many other primates, both adult male and female *R. avunculus* preferred horizontal and oblique supports during postural activities and by postural modes (Table 6.16). In this study, adult male and female *R. avunculus* only differed in the frequencies of support orientation use during displaying, and while standing and other postures. Studies of Fan *et al.* (2013), Gebo (1992), and Gebo and Chapman (1995b) found there were significant differences for males and females in the used support orientation.

Adult males and females significantly differed in use of support flexibility during resting, and while standing and other postures. Adult males used flexible supports more frequently than did females while adult females used stable supports more than did males. There were no previous studies on sex-based differences in support flexibility use for comparison with this study.

Summary

- Overall, adult male and female *R. avunculus* were significantly different during maintenance activities. There were significant differences between adult males and females during foraging, feeding and social behaviors, but no significant differences between males and females during traveling, resting and displaying. Adult females more frequently foraged, fed and participated in social behaviors than adult males.
- In locomotion, there were no significant differences between adult males and females during travel and foraging. The locomotion of both males and females was dominated by quadrupedalism, followed by leap, drop, arm-swing and other locomotion.
- In postures, there were only significant differences between adult males and females in overall postural behaviors, during rest and social behaviors. The postures of both adult males and females were dominated by sit, followed by stand, lie, cling and other postures.

Adult males and females differed significantly in stand during resting, and lie during social behavior.

- Adult males and females were significantly different in use of support size in both locomotion and postures. During travel and foraging, adult males used branches and trunks more often than females, while females used boughs, twigs and lianas more frequent than males. During resting and feeding, adult males used boughs and branches more frequently than females.
- There were significant differences between adult males and females in use of support flexibility. In locomotion, adult females used stable supports more frequently than did males during travel. In postures, adult females used stable supports more frequent than males during resting, feeding and displaying.
- Sex-related differences in body size influenced the positional behavior and support use of adult male and female *R. avunculus*, but did not follow consistently the predictions based on body size.

CHAPTER VII

AGE-BASED DIFFERENCES

7.1. Introduction

While primates are characterized by species-defined trajectories of growth and development, the degree to which positional behavior varies within species and during varying maintenance contexts is presently poorly understood. At present, studies of ontogenetic effects on primate positional behavior are rare and have largely focused on older juveniles (e.g., Bezanson, 2006b; Crompton, 1983; Doran, 1989; Wells and Turnquist, 2001; Workman and Covert, 2005) but still offer critical insight into how factors such as body mass, motor skills, and development trajectories affect ecological and dietary distinctions between adult and immature individuals (Garber, 2011). Based on current evidence, it appears that in many primate species, including taxa that are characterized by a relatively short juvenile period and those characterized by a relatively long juvenile period, immature animals exhibit adult-like patterns of positional behavior at a relatively early age (e.g., Bezanson, 2006b; Thorpe and Crompton, 2005, 2006). Lawler (2006) reported there were “no differences in locomotor behaviors or substrate use between yearling and adult Verreaux’s sifakas (*Propithecus verreauxi verreauxi*) in the Beza Mahafaly Special Reserve, Madagascar. Thus, data on apes, Old World monkeys, New World monkeys, and strepsirrhines provide only limited evidence for significant sex- and age-based differences in positional behavior and substrate use (Garber, 2011).

In this chapter, I discuss age-based differences in posture and locomotion and associated maintenance activities in *Rhinopithecus avunculus*. Specifically, I address the nature of these differences and the degree to which developmental timing and environment may influence positional behavior.

Hypotheses to test are the following:

Hypothesis 7.1: Similar to primates that have been studied, there is no significant difference in positional behavior and substrate use between adult and immature *R. avunculus*.

Hypothesis 7.2: If Hypothesis 7.1 is not supported, larger-bodied adults more frequently use suspensory behavior and less frequently leap than smaller-bodied immature individuals; adults more frequently use sitting and standing behaviors, and less frequently bipedal stand and cling.

Hypothesis 7.3: If Hypothesis 7.1 is not supported, given larger-bodied size, adults use larger substrates more commonly than immature individuals; also, while foraging in smaller substrates adults will more commonly use suspensory postures than immature individuals.

The questions addressed in this chapter are:

1) What are the ontogenetic patterns of positional behavior of *R. avunculus* across different behavioral contexts?
2) Do age-related differences in body size influence positional behavior and substrate use?
3) When do adult patterns of positional behavior appear during ontogeny in *R. avunculus*?

7.2. Methods

We lack clear age-categories for this species since it has never been held in captivity and there are no long-term field studies on habituated animals. In this study age categories of *Rhinopithecus avunculus* were based on morphological and behavioral differences and I use the following: Infant, Juvenile 1, Juvenile 2, and Adult. Field observations suggest that during the time of data collection the population of *Rhinopithecus avunculus* at Khau was approximately 100 and included at least 12 adult males, 25 adult females, 10 infants and the remaining were juveniles. Out of a total of 6,620 bouts, 3,507 were of Adult, 1,666 of Juvenile 2, 1,096 of Juvenile 1, and 351 of Infant.

I compared profiles for all postures and all locomotor behaviors and support use between infant, juvenile, and adult *R. avunculus* in Khau Ca Forest using the G-Tests of independence with the Bonferroni correction (MacDonald, 2008). All tests were two-tailed and performed using Microsoft Excel (see MacDonald, 2008).

7.3. Results

7.3.1. Overall Age-based Differences

All bouts of maintenance activities were allocated to one of six categories: travel, forage, rest, feed, social behaviors, and display. The most common activities were travel and rest (Table 7.1 and Figure 7.1). All age classes were significantly different during maintenance activities (G = 150.488, $p < 0.0001$). There were no significant differences between age classes during traveling (G = 0.648, n.s.), foraging (G = 10.924, n.s) and displaying (G = 4.135, n.s.); and significant age-based differences during resting (G = 23.751, $p < 0.001$), feeding (G = 30.658, $p < 0.001$) and social behaviors (G = 65.850, $p < 0.001$) (Table 7.1; Figure 7.1).

Though all age classes show the same trend by bouts (traveling > resting > feeding > foraging > socializing > displaying), there were some interclass differences for all maintenance activities include adult versus (vs.) juvenile 2 (G = 12.771, $p < 0.05$), Adult vs. Infant (G = 124.937, $p < 0.0001$), Juvenile 2 vs. Juvenile 1 (G = 16.038, $p < 0.01$), juvenile 2 vs. infant (G = 122.515, $p < 0.0001$), and juvenile 1 vs. infant (G = 84.265, $p < 0.0001$). Frequencies of traveling and resting tended to be greater among adults and juveniles. Feeding and foraging varied inconsistently across age classes. There were significant differences between adults and juveniles 2 versus infants in resting, feeding, foraging and social behaviors, and between juveniles 1 and infants in feeding and social behaviors (Table 7.2; Figure 7.1).

Quadrupedalism was the most frequent locomotor mode for all ages, followed by leap, climb, drop, arm-swing and other locomotion. Sit was the most common postural mode for all ages, followed by stand, lie, cling and other postures. There were significant age-based differences in overall locomotor and postural behaviors for *R. avunculus* (G = 88.994, p <

0.0001). There were overall age-based differences for arm-swing (G = 18.302 p < 0.01), cling (G = 18.405, p < 0.01) and other postures (G = 18.594, p < 0.01) (Table 7.3; Figure 7.2). There were some interclass differences for locomotor and postural modes include adults vs. juveniles 2 in arm-swing (G = 10.143, p < 0.05) and other postures (11.910, p < 0.05), adults vs. juveniles 1 in cling (G = 18.133, p < 0.01), adults vs. infants in other postures (G = 9.502, p < 0.05), and juveniles 2 vs. juvenile 1 in arm-swing (G = 13.360, p < 0.01 (Table 7.4; Figure 7.2).

Table 7.1. Maintenance activity budget of *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Travel	1,587	45.25%	744	44.66%	506	46.17%	149	42.45%	ns
Forage	82	2.34%	43	2.58%	24	2.19%	20	5.70%	ns
Rest	1,482	42.26%	695	41.72%	444	40.51%	83	23.65%	***
Feed	195	5.56%	109	6.54%	62	5.66%	52	14.81%	***
Display	78	2.22%	53	3.18%	24	2.19%	8	2.28%	ns
Social behaviors	83	2.37%	22	1.32%	36	3.28%	39	11.11%	***
Total	*3,507*	*100.00%*	*1,666*	*100.00%*	*1,096*	*100.00%*	*351*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and positional maintenance activities after comparisons using Bonferroni correction. n.s.: not significant, *** p < 0.001. Overall ages: G = 150.488 ***.

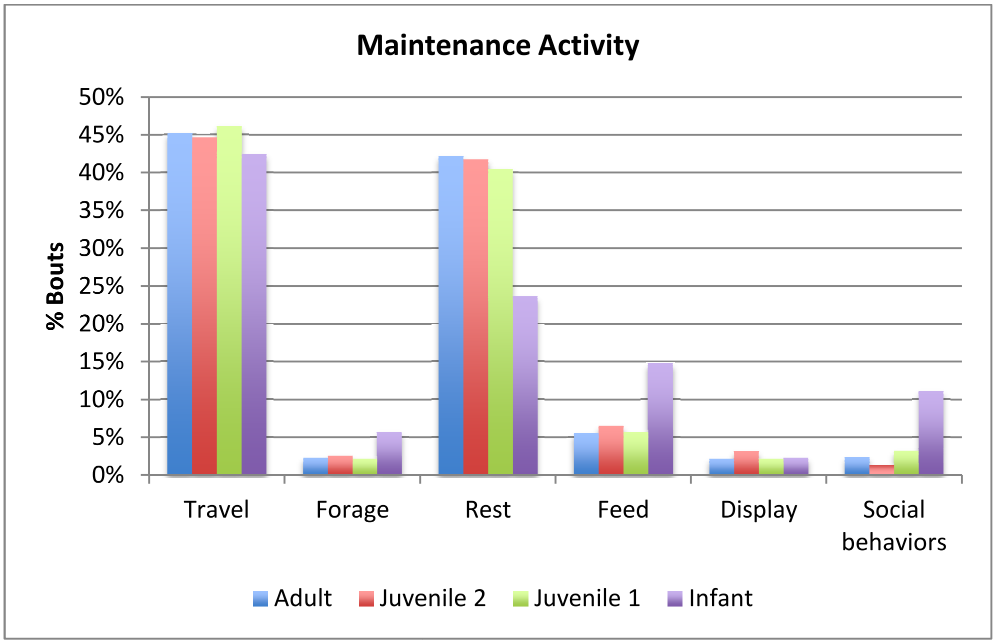

Figure 7.1. Frequencies of maintenance activity budget of infant, juvenile and adult *R. avunculus* in Khau Ca Forest

Table 7.2. G-tests of age-based differences in positional maintenance activities by *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Travel	0.061 n.s.	0.105 n.s.	0.393 n.s.	0.229 n.s.	0.224 n.s.	0.570 n.s.
Forage	0.266 n.s.	0.079 n.s.	10.217 **	0.412 n.s.	7.371 *	9.046 *
Rest	0.056 n.s.	0.434 n.s.	23.459 ***	0.165 n.s.	20.674 ***	17.165 ***
Feed	1.718 n.s.	0.013 n.s.	29.753 ***	0.798 n.s.	19.154 ***	22.565 ***
Display	3.832 n.s.	0.004 n.s.	0.004 n.s.	2.340 n.s.	0.815 n.s.	0.009 n.s.
Social behaviors	6.456 n.s.	2.507 n.s.	47.601 ***	11.550 *	62.395 ***	25.106 ***

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Overall age classes: G(Adult vs. Juvenile 2) = 12.771 *, G(Adult vs. Juvenile 1) = 3.442 n.s., G(Adult vs. Infants) = 124.937 ***, G(Juveniles 2 vs.1) = 16.038 **, G(Juveniles 2 vs. Infants) = 122.515 ***, G(Juvenile 1 vs. Infants) = 84.265 ***.

Table 7.3. Positional profiles of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Quadrupedalism	913	26.03%	382	22.93%	274	25.00%	79	22.51%	n.s.
Leap	239	6.81%	128	7.68%	80	7.30%	32	9.12%	n.s.
Climb	221	6.30%	98	5.88%	74	6.75%	19	5.41%	n.s.
Drop	171	4.88%	88	5.28%	60	5.47%	18	5.13%	n.s.
Arm-swing	95	2.71%	75	4.50%	21	1.92%	16	4.56%	**
Other locomotion	30	0.86%	16	0.96%	21	1.92%	5	1.42%	n.s.
Sit	1,537	43.83%	706	42.38%	449	40.97%	141	40.17%	n.s.
Stand	194	5.53%	75	4.50%	45	4.11%	18	5.13%	n.s.
Lie	38	1.08%	33	1.98%	19	1.73%	6	1.71%	n.s.
Cling	31	0.88%	25	1.50%	30	2.74%	5	1.42%	**
Other posture	38	1.08%	40	2.40%	23	2.10%	12	3.42%	**
Total	*3,507*	*100.00%*	*1,666*	*100.00%*	*1,096*	*100.00%*	*351*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and positional maintenance activities after comparisons using Bonferroni correction. n.s.: not significant, ** p < 0.01, *** p < 0.001. Overall ages: G = 88.994 ***.

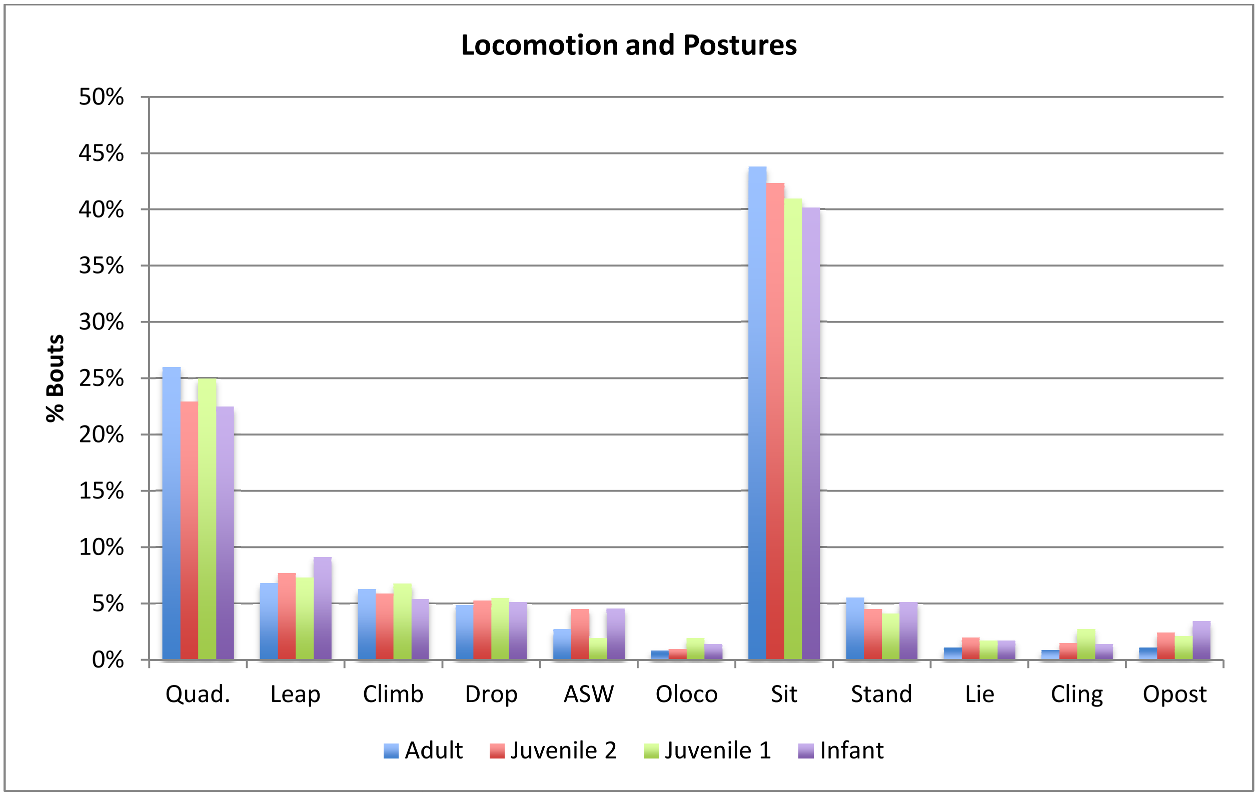

Figure 7.2. Frequencies of positional behaviors of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest.

Note. Quad.: Quadrupedalism combined quadrupedal walk and run, Oloco: Other locomotion, OPost: Other postures.

Table 7.4. G-tests of age-based differences in positional behavior of *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Quadrupedalism	3.543 n.s.	0.277 n.s.	1.287 n.s.	0.958 n.s.	0.018 n.s.	0.556 n.s.
Leap	1.104 n.s.	0.261 n.s.	2.062 n.s.	0.121 n.s.	0.669 n.s.	1.012 n.s.
Climb	0.306 n.s.	0.245 n.s.	0.398 n.s.	0.749 n.s.	0.106 n.s.	0.726 n.s.
Drop	0.351 n.s.	0.556 n.s.	0.039 n.s.	0.043 n.s.	0.012 n.s.	0.057 n.s.
Arm-swing	10.143 *	2.164 n.s.	3.170 n.s.	13.360 **	0.002 n.s.	6.200 n.s.
Other locomotion	0.137 n.s.	7.391 n.s.	0.976 n.s.	4.322 n.s.	0.545 n.s.	0.370 n.s.
Sit	0.384 n.s.	1.123 n.s.	0.705 n.s.	0.222 n.s.	0.240 n.s.	0.029 n.s.
Stand	2.250 n.s.	3.286 n.s.	0.092 n.s.	0.230 n.s.	0.229 n.s.	0.588 n.s.
Lie	6.156 n.s.	2.602 n.s.	0.952 n.s.	0.213 n.s.	0.112 n.s.	0.001 n.s.
Cling	3.719 n.s.	18.133 **	0.864 n.s.	4.844 n.s.	0.011 n.s.	2.081 n.s.
Other posture	11.910**	5.758 n.s.	9.502 *	0.262 n.s.	1.050 n.s.	1.726 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Overall age classes: G(Adult vs. Juvenile 2) = 41.949 ***, G(Adult vs. Juvenile 1) = 43.117 ***, G(Adult vs. Infants) = 21.158 *, G(Juveniles 2 vs.1) = 26.310 **, G(Juveniles 2 vs. Infants) = 3.210 n.s., G(Juvenile 1 vs. Infants) = 13.924 n.s.

Single and combined supports were used most frequently by all age classes. There were significant age-based differences in using support number ($G = 29.081$, $p < 0.001$), and by multi supports ($G = 15.019$, $p < 0.01$) (Table 7.5; Figure 7.3). There were significant differences of age classes, except Adults vs. Juveniles 2 in use of support number, and specifically the only interclass difference was between Juveniles 2 vs. Infants in using multi supports ($G = 9.630$, $p < 0.01$) (Table 7.6).

Branches and boughs were the most commonly used supports by all ages. There were significant differences between all ages and support size ($G = 224.892$, $p < 0.0001$), and by trunk ($G = 20.300$, $p < 0.01$), boughs ($G = 16.909$, $p < 0.01$) and twigs ($G = 140.128$, $p < 0.0001$) (Table 7.5; Figure 7.3). Adults, juveniles and infants differed in using support size overall, and by boughs and twigs mainly (Table 7.6). Larger animals tended to use larger supports more than smaller animals.

R. avunculus used horizontal supports most frequently, followed by oblique, vertical, terminal, and fork supports. There were significant differences of all ages and support orientation ($G = 79.035$, $p < 0.0001$), and by vertical support, ($G = 18.505$, $p < 0.01$), terminal supports ($G = 17.647$, $p < 0.001$) and forks (14.028, $p< 0.05$) (Table 7.5; Figure 7.3). Adults, juveniles and infants differed in using support orientation overall, and by vertical and terminal supports mainly (Table 7.6). Larger animals tended to use vertical and terminal supports less than smaller animals.

Stable supports were used more frequently than flexible supports by all ages. There were significant differences of overall ages and support flexibility ($G = 30.941$, $p < 0.0001$) (Table 7.5; Figure 7.3). Adults, juveniles and infants differed in using support flexibility overall, and by stable and flexible supports for Adults vs. Juveniles 2, and Juvenile 2 vs. 1 (Table 7.6).

Table 7.5. Support use of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Support number:									
Single	2903	82.78%	1342	80.55%	898	81.93%	285	81.20%	n.s
Combined	440	12.55%	227	13.63%	152	13.87%	61	17.38%	n.s
Multi	113	3.22%	71	4.26%	24	2.19%	4	1.14%	**
Network	51	1.45%	26	1.56%	22	2.01%	1	0.28%	n.s
Subtotal	*3507*	*100.00%*	*1666*	*100.00%*	*1096*	*100.00%*	*351*	*100.00%*	
Support size:									
Trunk	62	1.77%	11	0.66%	25	2.28%	1	0.28%	***
Bough	678	19.33%	253	15.19%	186	16.97%	41	11.68%	**
Branch	2544	72.54%	1266	75.99%	761	69.43%	198	56.41%	n.s
Twig	188	5.36%	111	6.66%	100	9.12%	103	29.34%	***
Liana	35	1.00%	25	1.50%	24	2.19%	8	2.28%	n.s
Subtotal	*3507*	*100.00%*	*1666*	*100.00%*	*1096*	*100.00%*	*351*	*100.00%*	
Support orientation:									
Horizontal	1754	50.01%	726	43.58%	482	43.98%	184	52.42%	n.s
Oblique	1291	36.81%	662	39.74%	397	36.22%	101	28.77%	n.s
Vertical	219	6.24%	128	7.68%	106	9.67%	39	11.11%	**
Terminal	117	3.34%	68	4.08%	68	6.20%	23	6.55%	**
Fork	126	3.59%	82	4.92%	43	3.92%	4	1.14%	*
Subtotal	*3507*	*100.00%*	*1666*	*100.00%*	*1096*	*100.00%*	*351*	*100.00%*	
Support flexibility:									
Flexible	1600	45.62%	883	53.00%	491	44.80%	182	51.85%	*
Stable	1907	54.38%	783	47.00%	605	55.20%	169	48.15%	*
Subtotal	*3507*	*100.00%*	*1666*	*100.00%*	*1096*	*100.00%*	*351*	*100.00%*	

Note. The last column represents significance of age-based differences in support use after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Ages vs. support use: G(number) = 29.081 ***, G(size) = 224.892 ***, G(orientation) = 79.035 ***, G(flexibility) = 30.941 ***.

Table 7.6. G-tests of age-based difference in support use by *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Support number:	**5.107 n.s.**	**5.917 ***	**15.842 *****	**9.693 ***	**17.518 *****	**10.692 ***
Single	0.376 n.s.	0.039 n.s.	0.053 n.s.	0.086 n.s.	0.008 n.s.	0.009 n.s.
Combined	0.894 n.s.	0.987 n.s.	4.587 n.s.	0.025 n.s.	2.359 n.s.	1.859 n.s.
Multi	3.210 n.s.	3.117 n.s.	5.731 n.s.	8.487 n.s.	9.630 **	1.672 n.s.
Network	0.084 n.s.	1.500 n.s.	4.597 n.s.	0.735 n.s.	4.838 n.s.	6.753 n.s.
Support size:	**29.762 *****	**30.306 *****	**185.431 *****	**25.118 *****	**127.004 *****	**86.359 *****
Trunk	11.099 **	1.092 n.s.	6.283 n.s.	12.849 **	0.815 n.s.	8.143 **
Bough	9.469 **	2.146 n.s.	9.818 **	1.134 n.s.	2.274 n.s.	4.416 n.s.
Branch	1.043 n.s.	0.660 n.s.	7.506 *	2.254 n.s.	9.726 **	4.306 n.s.
Twig	3.052 n.s.	16.225 **	135.331 ***	4.779 n.s.	93.350 ***	56.719 ***
Liana	2.328 n.s.	8.073 *	3.662 n.s.	1.703 n.s.	0.965 n.s.	0.009 n.s.
Support orientation:	**22.377 *****	**35.120 *****	**31.061 *****	**12.611 ***	**35.036 *****	**16.991 ****
Horizontal	6.747 n.s.	4.344 n.s.	0.241 n.s.	0.017	3.286 n.s.	2.713 n.s.
Oblique	1.836 n.s.	0.058 n.s.	4.560 n.s.	1.552	7.301 *	3.353 n.s.
Vertical	3.185 n.s.	12.007 **	8.900 *	2.802 n.s.	3.488 n.s.	0.487 n.s.
Terminal	1.655 n.s.	14.814 **	7.194 *	5.636 n.s.	3.377 n.s.	0.048 n.s.
Fork	4.604 n.s.	0.236 n.s.	7.302 *	1.419 n.s.	12.587 **	7.664 *
Support flexibility:	**24.630 *****	**0.229 n.s.**	**4.964 ***	**17.814 *****	**154.000 *****	**5.305 ***
Flexible	8.462 *	0.086 n.s.	1.750 n.s.	6.072 *	0.048 n.s.	1.878 n.s.
Stable	7.968 *	0.067 n.s.	1.563 n.s.	5.812 *	0.055 n.s.	1.663 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

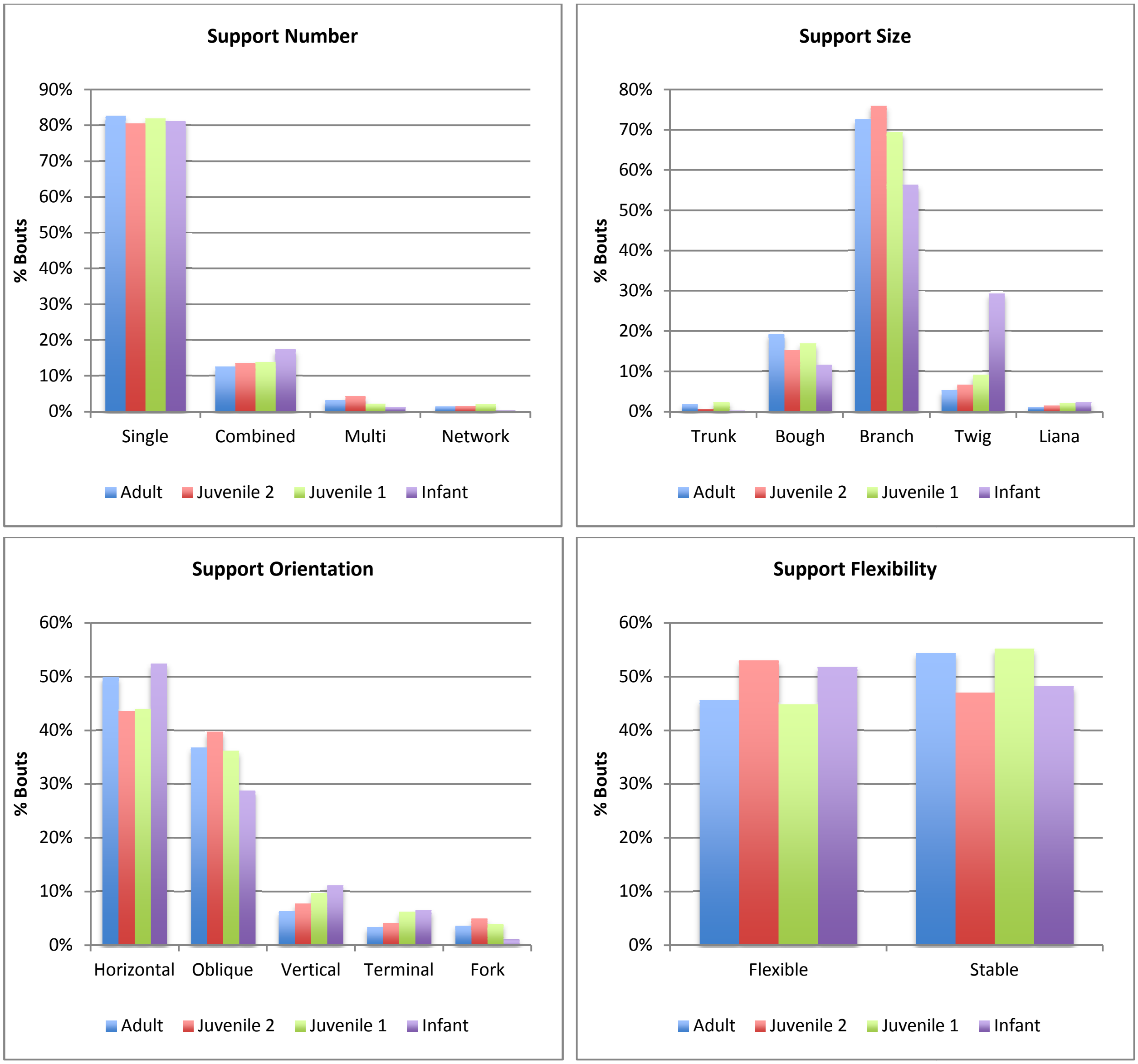

Figure 7.3. Support use of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest

7.3.2. Age-based Differences During Travel

During travel, all infant, juvenile and adult *R. avunculus* employed six main locomotor categories including quadrupelalism, leap, climb, drop, arm-swing and other locomotion (Table 7.7). All age classes were significantly different during travel overall ($G = 34.319$, $p < 0.01$).

Quadrupedalism was the most frequent locomotor mode in travel repertoire (A: 53.69%; J2: 48.12%; J1: 50.79%; I: 45.64%), followed by leap (A: 14.93%; J2: 17.20%; J1: 15.81%; I: 20.81%), climb (A: 13.17%; J2: 11.96%; J1: 14.03%; I: 12.08%), drop (A: 10.59%; J2: 11.16%; J1: 11.26%; I: 10.07%), arm-swing (A: 5.86%; J2: 9.41%; J1: 3.95%; I: 8.05%) and other locomotion (A: 1.76%; J2: 2.15%; J1: 4.15%; I: 3.36%). The only significant differences between ages in travel occurred in the use of arm-swing ($G = 14.931$, $p < 0.05$) that Juveniles 2 and Infants more frequently used arm-swing than Adults vs. Juveniles 1 (Table 7.7). In the interclass comparison, there were significant differences between Adults vs. Juveniles 2 by arm-swing ($G = 8.086$, $p < 0.05$), Adults vs. Juveniles 1 by other locomotion ($G = 7.993$, $p < 0.05$), and Juveniles 2 vs. 1 by arm-swing ($G = 12.628$, $p < 0.01$) and other locomotion ($G = 3.855$, $p < 0.05$) (Table 7.8).

Table 7.7. Locomotor profiles during travel by infant, juvenile, and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Quadrupedalism	852	53.69%	358	48.12%	257	50.79%	68	45.64%	n.s.
Leap	237	14.93%	128	17.20%	80	15.81%	31	20.81%	n.s.
Climb	209	13.17%	89	11.96%	71	14.03%	18	12.08%	n.s.
Drop	168	10.59%	83	11.16%	57	11.26%	15	10.07%	n.s.
Arm-swing	93	5.86%	70	9.41%	20	3.95%	12	8.05%	*
Other locomotion	28	1.76%	16	2.15%	21	4.15%	5	3.36%	n.s.
Total	*1,587*	*100.00%*	*744*	*100.00%*	*506*	*100.00%*	*149*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and positional modes during travel after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$. Overall ages: $G = 34.319$ **.

Table 7.8. G-tests of age-based differences in locomotor behaviors during travel by *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Quadrupedalism	2.028 n.s.	0.402 n.s.	1.155 n.s.	0.292 n.s.	0.110 n.s.	0.423 n.s.
Leap	1.415 n.s.	0.167 n.s.	2.368 n.s.	0.303 n.s.	0.731 n.s.	1.371 n.s.
Climb	0.519 n.s.	0.168 n.s.	0.112 n.s.	0.884 n.s.	0.001 n.s.	0.293 n.s.
Drop	0.137 n.s.	0.147 n.s.	0.032 n.s.	0.003 n.s.	0.124 n.s.	0.138 n.s.
Arm-swing	8.086 *	2.639 n.s.	0.929 n.s.	12.628 **	0.236 n.s.	3.337 n.s.
Other locomotion	0.384 n.s.	7.993 *	1.474 n.s.	3.855 *	0.678 n.s.	0.183 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$. Overall age classes: G(Adult vs. Juvenile 2) = 14.514 *, G(Adult vs. Juvenile 1) = 12.157 *, G(Adult vs. Infants) = 7.169 n.s., G(Juveniles 2 vs.1) = 19.230 **, G(Juveniles 2 vs. Infants) = 2.119 n.s., G(Juvenile 1 vs. Infants) = 6.438 n.s.

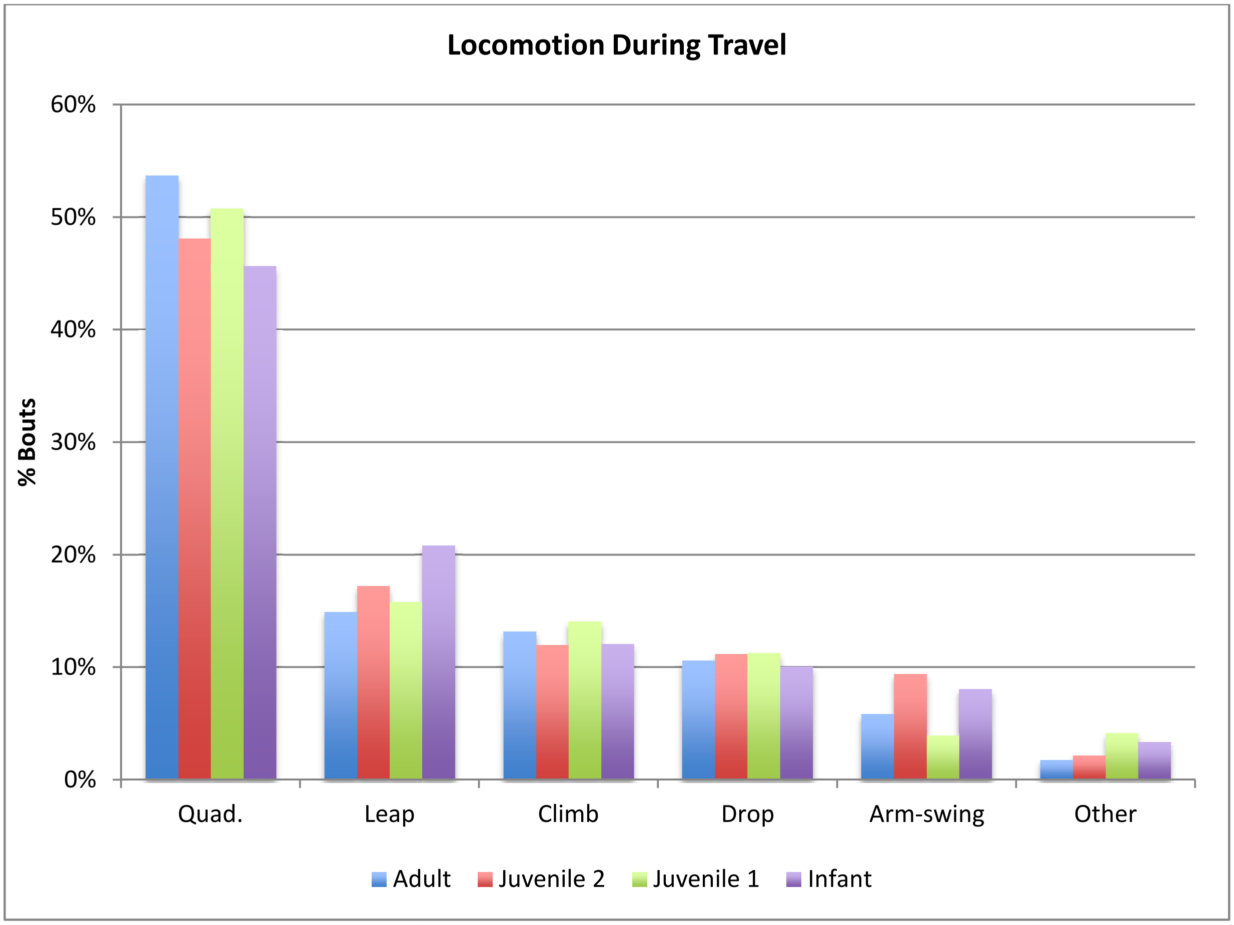

Figure 7.4. Frequencies of positional behaviors during travel of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest.

Note. Quad.: Quadrupedalism combined quadrupedal walk and run, Other: Other locomotion.

During travel, single and combined supports were used most frequently by all age classes. There were no significant age-based differences in using support number overall (G = 15.452 n.s.), and by each support number use (Table 7.9; Figure 7.5). There was only interclass difference between Adults and Infants in support number use overall ($G = 8.531$, $p < 0.05$). Older animals tended to use single, multi and network supports more frequently than did younger animals, while younger animals used combined supports more frequently (Table 7.10).

Branches and boughs were the most commonly used support types by all ages during travel. There were significant differences between all ages and support size overall ($G = 74.709$, $p < 0.0001$), and by twigs ($G = 39.781$, $p < 0.001$) (Table 7.9; Figure 7.5). Adults, juveniles and infants differed in using boughs and twigs mainly (Table 7.10). Larger-sized older animals tended to use larger support more than smaller-sized younger animals. There were significant interclass differences in use of support size overall. Specifically, for each type of support size, there were significant differences between Adults vs. Juveniles 2 by trunks, Adults vs. Infants by twigs, and Juveniles 1 and 2 vs. Infants by twigs (Table 7.10).

R. avunculus used horizontal supports most frequently, followed by oblique, vertical, terminal, and forked supports. There was significant difference of all ages and support orientation overall ($G = 26.426$, $p < 0.01$). Adults, juveniles and infants differed in using vertical and terminal supports mainly (Table 7.9; Figure 7.5). Larger animals tended to use vertical and terminal supports less than smaller animals. Statistically, there were only significant interclass differences for Adults vs. Infants, and Juveniles 2 vs. Infants in use of support orientation overall. For each type of support orientation, adults and infants significantly differed in use of vertical and terminal supports; adults used more verticals and fewer terminals than did infants (Table 7.10).

There were significant differences of overall ages and support flexibility ($G = 18.084$, $p < 0.001$). Stable supports were used slightly different between age categories. Older animals tended to use flexible supports more frequently than did younger animals (Table 7.9; Figure 7.5). There were significant interclass differences for Adults vs. Infants ($G = 13.395$, $p < 0.001$), Juveniles 2 vs. 1 (G = 13.544, $p < 0.001$), and Juveniles 2 vs. Infants (G = 4.215, $p < 0.05$) in choosing support flexibility (Table 7.10).

Table 7.9. Support use during travel by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Support number:									
Single	1,255	79.08%	558	75.00%	395	78.06%	109	73.15%	n.s.
Combined	246	15.50%	140	18.82%	92	18.18%	36	24.16%	n.s.
Multi	67	4.22%	36	4.84%	14	2.77%	3	2.01%	n.s.
Network	19	1.20%	10	1.34%	5	0.99%	1	0.67%	n.s.
Subtotal	*1,587*	*100.00%*	*744*	*100.00%*	*506*	*100.00%*	*149*	*100.00%*	
Support size:									
Trunk	39	2.46%	7	0.94%	11	2.17%	1	0.67%	n.s.
Bough	295	18.59%	103	13.84%	86	17.00%	19	12.75%	n.s.
Branch	1,148	72.34%	580	77.96%	354	69.96%	90	60.40%	n.s.
Twig	94	5.92%	44	5.91%	45	8.89%	36	24.16%	***
Liana	11	0.69%	10	1.34%	10	1.98%	3	2.01%	n.s.
Subtotal	*1,587*	*100.00%*	*744*	*100.00%*	*506*	*100.00%*	*149*	*100.00%*	
Support orientation:									
Horizontal	692	43.60%	301	40.46%	200	39.53%	54	36.24%	n.s.
Oblique	627	39.51%	308	41.40%	197	38.93%	50	33.56%	n.s.
Vertical	173	10.90%	90	12.10%	73	14.43%	30	20.13%	n.s.
Terminal	63	3.97%	29	3.90%	27	5.34%	14	9.40%	n.s.
Fork	32	2.02%	16	2.15%	9	1.78%	1	0.67%	n.s.
Subtotal	*1,587*	*100.00%*	*744*	*100.00%*	*506*	*100.00%*	*149*	*100.00%*	
Support flexibility:									
Flexible	795	50.09%	433	58.20%	241	47.63%	73	48.99%	n.s.
Stable	792	49.91%	311	41.80%	265	52.37%	76	51.01%	n.s.
Subtotal	*1,587*	*100.00%*	*744*	*100.00%*	*506*	*100.00%*	*149*	*100.00%*	

Note. The last column represents significance of age-based differences in support use during travel after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Ages vs. support use: G(number) = 15.452 n.s., G(size) = 74.709 ***, G(orientation) = 26.426 **, G(flexibility) = 18.084 ***.

Table 7.10. G-tests of age-based differences in support use during travel by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Support number:	**4.897 n.s.**	**4.125 n.s.**	**8.531 ***	**4.145 n.s.**	**5.023 n.s.**	**2.770 n.s.**
Single	0.616 n.s.	0.028 n.s.	0.352 n.s.	0.210 n.s.	0.033 n.s.	0.207 n.s.
Combined	2.814 n.s.	1.426 n.s.	4.679 n.s.	0.055 n.s.	1.408 n.s.	1.661 n.s.
Multi	0.411 n.s.	2.183 n.s.	1.924 n.s.	3.260 n.s.	2.369 n.s.	0.261 n.s.
Network	0.086 n.s.	-	0.376 n.s.	0.322 n.s.	0.525 n.s.	0.134 n.s.
Support size:	**18.048 ****	**11.167 ***	**50.662 *****	**12.077 ***	**40.851 *****	**23.264 *****
Trunk	6.626 *	0.129 n.s.	2.515 n.s.	3.058 n.s.	0.108 n.s.	1.730 n.s.
Bough	5.956 n.s.	0.460 n.s.	2.347 n.s.	1.697 n.s.	0.097 n.s.	1.184 n.s.
Branch	1.224 n.s.	0.177 n.s.	1.702 n.s.	1.491 n.s.	3.158 n.s.	0.960 n.s.
Twig	0.0001 n.s.	4.453 n.s.	36.221 ***	3.434 n.s.	31.226 ***	16.218 ***
Liana	2.212 n.s.	5.358 n.s.	2.135 n.s.	0.727 n.s.	0.344 n.s.	0.0008 n.s.
Support orientation:	**2.322 n.s.**	**7.127 n.s.**	**20.154 *****	**3.341 n.s.**	**16.174 ****	**7.338 n.s.**
Horizontal	0.836 n.s.	1.074 n.s.	1.283 n.s.	0.047 n.s.	0.410 n.s.	0.235 n.s.
Oblique	0.319 n.s.	0.023 n.s.	0.942 n.s.	0.324 n.s.	1.443 n.s.	0.663 n.s.
Vertical	0.569 n.s.	3.448 n.s.	7.305 *	1.097 n.s.	4.640 n.s.	1.927 n.s.
Terminal	0.0064 n.s.	1.517 n.s.	6.662 *	1.309 n.s.	6.105 n.s.	2.575 n.s.
Fork	0.043 n.s.	0.111 n.s.	1.667 n.s.	0.207 n.s.	1.790 n.s.	1.092 n.s.
Support flexibility:	**13.395 *****	**0.934 n.s.**	**0.066 n.s.**	**13.544 *****	**4.251 ***	**0.086 n.s.**
Flexible	4.041 n.s.	0.319 n.s.	0.022 n.s.	4.134 n.s.	1.248 n.s.	0.030 n.s.
Stable	4.915 n.s.	0.304 n.s.	0.022 n.s.	4.920 n.s.	1.599 n.s.	0.027 n.s.

Note. The last column represents significance of age-based differences in support use during travel after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

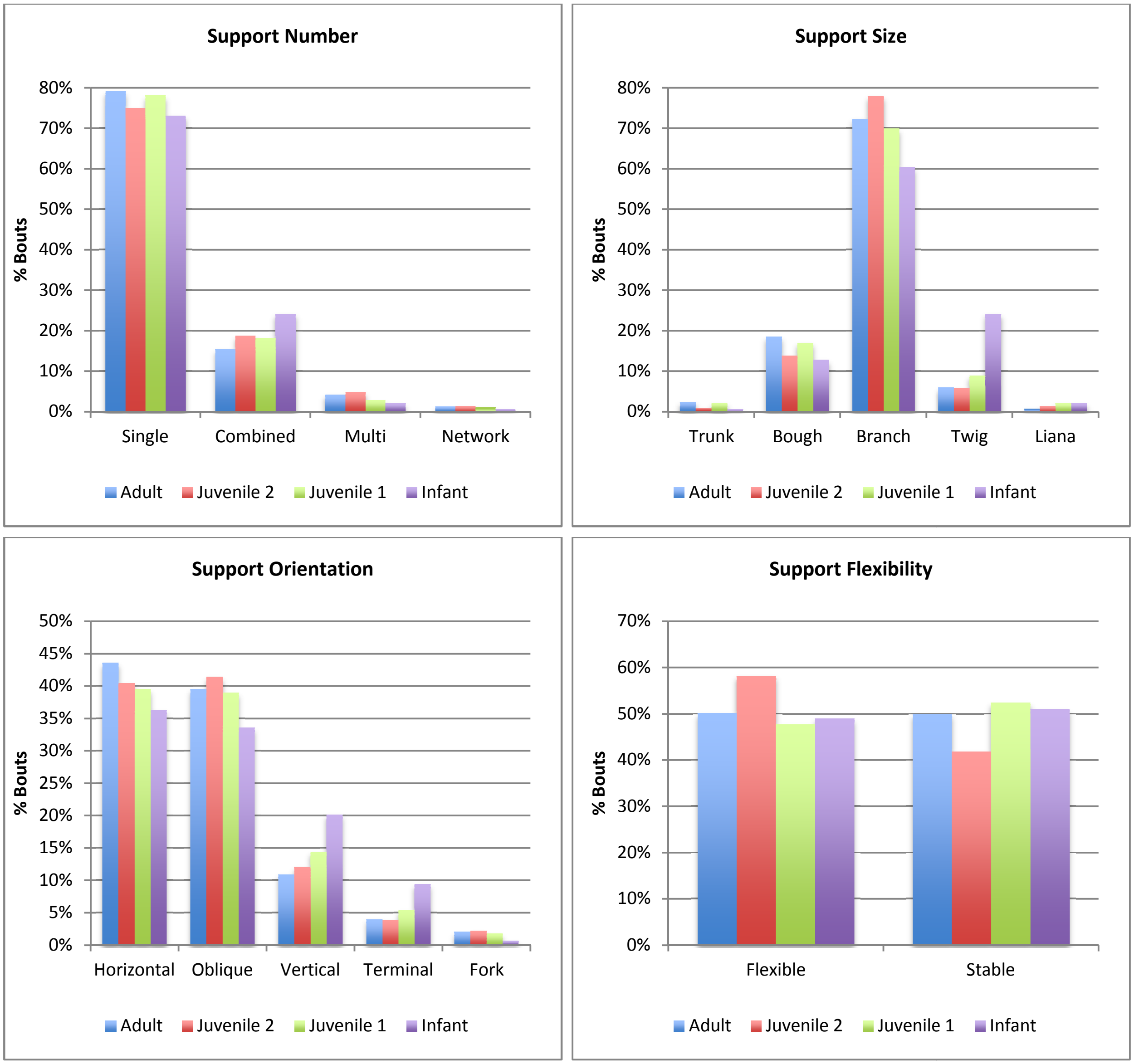

Figure 7.5. Support use during travel by infant, juvenile, and adult *R. avunculus* in Khau Ca Forest

7.3.3. Age-based Differences During Feeding and Foraging

All age classes were significantly different in positional modes during foraging and feeding overall (G = 46.801, $p < 0.05$). Quadrupedalism was the most frequent locomotor mode during foraging (A: 22.02%; J2: 15.97%; J1: 19.77%; I: 15.28%); sitting was the most postural mode during feeding (A: 63.54%; J2: 59.87%; J1: 56.98%; I: 55.56%). The only significant differences between ages in foraging and feeding occurred in the use of stand (G = 11.717, $p < 0.05$) with frequencies decreasing as ages increases (Table 7.11; Figure 7.6). In the interclass comparison, there were significant differences in positional modes during foraging and feeding between Adults vs. Infants (G = 27.213, $p < 0.01$), and by stand (G = 10.549, $p < 0.05$) (Table 7.12).

Table 7.11. Positional profiles during foraging and feeding by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Quadrupedalism	61	22.02%	24	15.79%	17	19.77%	11	15.28%	n.s.
Leap	2	0.72%	-	-	-	-	1	1.39%	n.s.
Climb	12	4.33%	9	5.92%	3	3.49%	1	1.39%	n.s.
Drop	3	1.08%	5	3.29%	3	3.49%	3	4.17%	n.s.
Arm-swing	2	0.72%	5	3.29%	1	1.16%	4	5.56%	n.s.
Other locomotion	2	0.72%	-	-	-	-	-	-	n.s.
Sit	176	63.54%	91	59.87%	49	56.98%	40	55.56%	n.s.
Stand	2	0.72%	2	1.32%	3	3.49%	6	8.33%	*
Cling	4	1.44%	5	3.29%	2	2.33%	-	-	n.s.
Lie	-	-	1	0.66%	1	1.16%	-	-	n.s.
Other posture	13	4.69%	10	6.58%	7	8.14%	6	8.33%	n.s.
Total	*277*	*100.00%*	*152*	*100.00%*	*86*	*100.00%*	*72*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and positional modes during foraging and feeding after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$. Overall ages: G = 46.801 *.

Table 7.12. G-tests of age-based differences in positional behavior during foraging and feeding by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Quadrupedalism	1.674 n.s.	0.131 n.s.	1.136 n.s.	0.421 n.s.	0.007 n.s.	0.383 n.s.
Leap	1.745 n.s.	1.078 n.s.	0.259 n.s.	-	2.261 n.s.	1.564 n.s.
Climb	0.469 n.s.	0.113 n.s.	1.603 n.s.	0.652 n.s.	2.652 n.s.	0.706 n.s.
Drop	2.369 n.s.	1.908 n.s.	2.486 n.s.	0.006 n.s.	0.099 n.s.	0.046 n.s.
Arm-swing	3.686 n.s.	0.141 n.s.	5.783 n.s.	1.089 n.s.	0.568 n.s.	2.427 n.s.
Other locomotion	1.745 n.s.	1.078 n.s.	0.921 n.s.	-	-	-
Sit	0.132 n.s.	0.289 n.s.	0.377 n.s.	0.049 n.s.	0.099 n.s.	0.009 n.s.
Stand	0.351 n.s.	2.942 n.s.	10.549 *	1.146 n.s.	5.943 n.s.	1.536 n.s.
Cling	1.477 n.s.	0.280 n.s.	1.837 n.s.	0.175 n.s.	3.826 n.s.	2.412 n.s.
Lie	2.071 n.s.	2.871 n.s.	-	0.159 n.s.	0.773 n.s.	1.211 n.s.
Other posture	0.600 n.s.	1.219 n.s.	1.178 n.s.	0.171 n.s.	0.191 n.s.	0.002 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant. Overall age classes: G(Adult vs. Juvenile 2) = 16.937 n.s., G(Adult vs. Juvenile 1) = 12.441 n.s., G(Adult vs. Infants) = 27.213 **, G(Juveniles 2 vs.1) = 4.070 n.s., G(Juveniles 2 vs. Infants) = 16.909 n.s., G(Juvenile 1 vs. Infants) = 10.581 n.s.

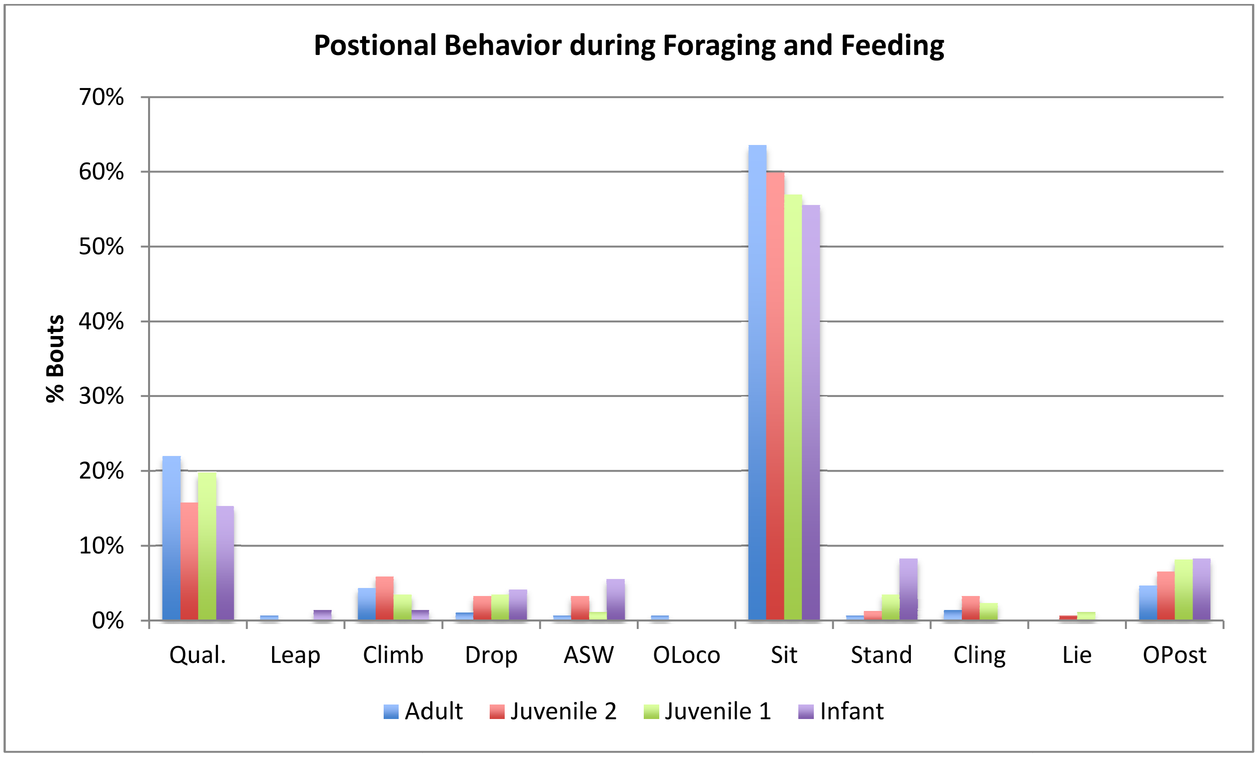

Figure 7.6. Frequencies of positional behaviors of infant, juvenile, and adult *R. avunculus* in Khau Ca Forest.

Note. Quad.: Quadrupedalism combined quadrupedal walk and run, ASW: arm-swing, Other: Other locomotion.

There were significant age-based differences in support use during foraging and feeding by all main support categories including support number (G = 51.195, $p < 0.001$), support size (G = 44.757, $p < 0.001$), support orientation (G = 34.030, $p < 0.001$) and support flexibility (G = 10.356, $p < 0.05$).

During foraging and feeding, single and combined supported were used by all age categories while multi and network supports were used only by adults and juveniles. There were significant difference between adults and juveniles in use of multi supports (G = 18.544, $p < 0.01$) and network supports (G = 15.273, $p < 0.01$); adults and juvenile 2 used multi support more frequently and network supports less than juveniles 1 (Table 7.13; Figure 7.7). Significantly interclass differences were seen for Adults vs. Infants, Juveniles 1 and 2 vs. Infants in support number use overall, and by multi and network supports (Table 7.14).

Branches and twigs were used most often by all ages. The frequencies of branch use increased by age while the frequencies of twig use decreased by age. All age categories differed significantly in twig use (G = 11.482, $p < 0.05$). Trunks, boughs and liana were less frequently used (Table 7.13; Figure 7.7). Significant age-based differences were seen between age classes with exception of Adults vs. Juveniles 2 in support size use overall. Specifically, by support size types, there were significant differences between Adults vs. Juveniles 2 by trunks (G = 6.918, $p < 0.05$), Adults vs Juveniles 1 by boughs (G = 8.441, $p < 0.05$, Adults vs. Infants (G = 10.373, $p < 0.01$) and Juveniles vs. Infants (G = 8.103, $p < 0.05$) by twigs (Table 7.14).

Horizontal and oblique supports were used most frequently by all ages. Terminal supports were also used quite frequently because *R. avunculus*' foods are mainly distributed on terminal supports. Vertical and forked supports were rarely used during foraging and feeding by all ages. There were significant differences in support orientation use between Adults vs. Juveniles 2 (10.765, $P < 0.05$), Adults vs. Infants (G = 12.635, $p < 0.05$), and Juveniles 1 vs. Infants (G = 16.555, $p < 0.01$).

Flexible supports were used more frequently by all ages (Table 7.13; Figure 7.7). There were significant differences in use of support flexibility between Juveniles 2 vs. Infants (G = 8.379, p < 0.01) and Juveniles 1 vs. Infants (G = 6.418, p < 0.05) (Table 7.14).

Table 7.13. Support use during feeding and foraging by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Support number:									
Single	146	52.71%	80	52.63%	41	47.67%	60	83.33%	n.s.
Combined	80	28.88%	34	22.37%	26	30.23%	12	16.67%	n.s.
Multi	30	10.83%	24	15.79%	6	6.98%	-	-	*
Network	21	7.58%	14	9.21%	13	15.12%	-	-	*
Subtotal	*277*	*100.00%*	*152*	*100.00%*	*86*	*100.00%*	*72*	*100.00%*	
Support size:									
Trunk	8	2.89%	-	-	3	3.49%	-	-	n.s.
Bough	16	5.78%	7	4.61%	-	-	3	4.17%	n.s.
Branch	171	61.73%	98	64.47%	47	54.65%	29	40.28%	n.s.
Twig	66	23.83%	37	24.34%	27	31.40%	38	52.78%	*
Liana	16	5.78%	10	6.58%	9	10.47%	2	2.78%	n.s.
Subtotal	*277*	*100.00%*	*152*	*100.00%*	*86*	*100.00%*	*72*	*100.00%*	
Support orientation:									
Horizontal	147	53.07%	61	40.13%	36	41.86%	52	72.22%	n.s.
Oblique	68	24.55%	42	27.63%	25	29.07%	12	16.67%	n.s.
Vertical	12	4.33%	17	11.18%	6	6.98%	3	4.17%	n.s.
Terminal	40	14.44%	26	17.11%	18	20.93%	5	6.94%	n.s.
Fork	10	3.61%	6	3.95%	1	1.16%	-	-	n.s.
Subtotal	*277*	*100.00%*	*152*	*100.00%*	*86*	*100.00%*	*72*	*100.00%*	
Support flexibility:									
Flexible	220	79.42%	131	86.18%	74	86.05%	50	69.44%	n.s.
Stable	57	20.58%	21	13.82%	12	13.95%	22	30.56%	n.s.
Subtotal	*277*	*100.00%*	*152*	*100.00%*	*86*	*100.00%*	*72*	*100.00%*	

Note. The last column represents significance of age-based differences in support use during foraging and feeding after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Ages vs. support use: G(number) = 51.195 ***, G(size) = 44.757 ***, G(orientation) = 34.030 ***, G(flexibility) = 10.356 *.

Table 7.14. G-tests of age-based differences in support use during feeding and foraging by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Support number:	**3.781 n.s.**	**4.996 n.s.**	**35.497 *****	**6.924 n.s.**	**37.299 *****	**33.975 *****
Single	0.0001 n.s.	0.218 n.s.	5.073 n.s.	0.178 n.s.	4.250 n.s.	4.741 n.s.
Combined	1.278 n.s.	0.031 n.s.	2.915 n.s.	1.045 n.s.	0.670 n.s.	2.510 n.s.
Multi	1.645 n.s.	0.974 n.s.	13.233 ***	3.332 n.s.	17.439 ***	7.115 *
Network	0.290 n.s.	3.227 n.s.	9.390 **	1.457 n.s.	10.463 **	14.983 ***
Support size:	**7.487 n.s.**	**12.590 ***	**24.045 *****	**15.267 ****	**17.862 ****	**18.086 ****
Trunk	6.918 *	0.073 n.s.	3.650 n.s.	6.042 n.s.	-	3.603 n.s.
Bough	0.244 n.s.	8.441 *	0.276 n.s.	6.164 n.s.	0.020 n.s.	4.649 n.s.
Branch	0.072 n.s.	0.353 n.s.	3.274 n.s.	0.553 n.s.	3.503 n.s.	1.156 n.s.
Twig	0.009 n.s.	1.104 n.s.	10.373 **	0.781 n.s.	8.103 *	3.072 n.s.
Liana	0.097 n.s.	1.768 n.s.	1.100 n.s.	0.927 n.s.	1.414 n.s.	3.444 n.s.
Support orientation:	**10.765 ***	**6.281 n.s.**	**12.635 ***	**3.240 n.s.**	**2.375 n.s.**	**16.555 ****
Horizontal	2.373 n.s.	1.150 n.s.	2.161 n.s.	0.028 n.s.	6.144 n.s.	4.151 n.s.
Oblique	0.286 n.s.	0.402 n.s.	1.379 n.s.	0.031 n.s.	2.125 n.s.	2.158 n.s.
Vertical	6.011 n.s.	0.812 n.s.	0.0035 n.s.	0.969 n.s.	2.863 n.s.	0.528 n.s.
Terminal	0.386 n.s.	1.389 n.s.	2.585 n.s.	0.360 n.s.	3.674 n.s.	4.999 n.s.
Fork	0.029 n.s.	-	4.548 n.s.	1.633 n.s.	4.579 n.s.	1.211 n.s.
Support flexibility:	**3.122 n.s.**	**1.975 n.s.**	**3.086 n.s.**	**0.001 n.s.**	**8.379 ****	**6.418 ***
Flexible	0.298 n.s.	0.193 n.s.	0.431 n.s.	0.000 n.s.	0.975 n.s.	0.781 n.s.
Stable	2.196 n.s.	1.380 n.s.	1.874 n.s.	0.001 n.s.	5.507 *	4.144 n.s.

Note. The last column represents significance of age-based differences in support use during foraging and feeding after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

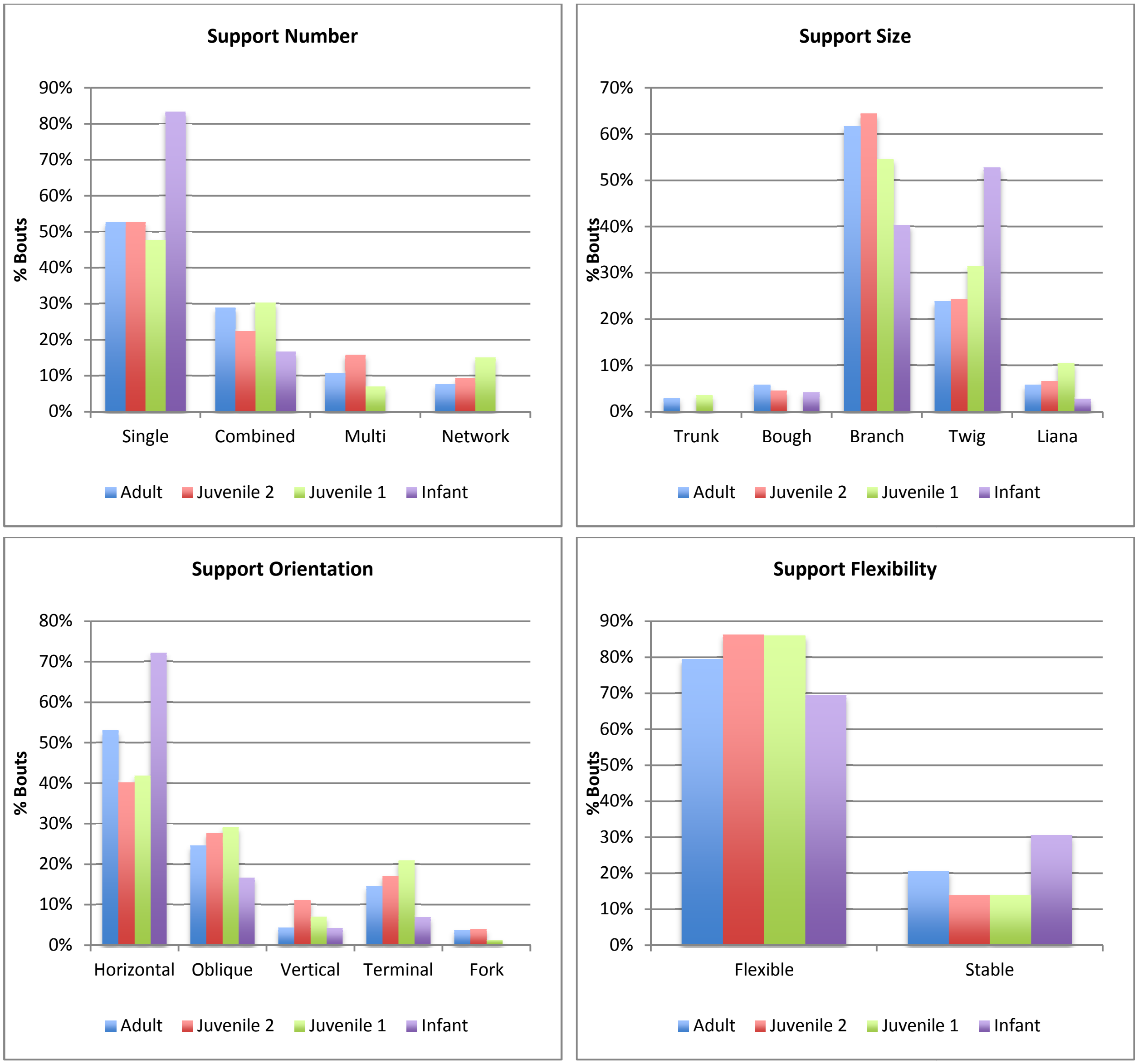

Figure 7.7. Frequencies of support use during foraging and feeding by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

7.3.4. Age-based Differences During Resting

During resting, all infant, juvenile and adult *R. avunculus* employed five main postural categories (sit, stand, lie, cling and other posture). All age classes were significantly different during resting overall ($G = 45.821$, $p < 0.01$). Sit was the most frequent postural mode during resting (A: 84.35%; J2: 82.73%; J1: 81.31%; I: 81.93%), followed by stand (A: 10.73%; J2: 7.19%; J1: 7.88%; I: 8.43%), lie (A: 1.82%; J2: 4.03%; J1: 2.93%; I: 2.41%), cling (A: 1.69%; J2: 2.45%; J1: 5.41%; I: 6.02%), and other posture (A: 1.42%; J2: 3.60%; J1: 2.48%; I: 1.20%) (Table 7.15). The only significant differences between ages in resting occurred in the use of cling ($G = 17.875$, $p < 0.001$) that younger animals more frequently used cling than older animals (Table 7.15). In the interclass comparison, significant differences were seen between Adult vs. Juvenile 2 ($G = 26.288$, $p < 0.001$), and Adult vs. Juvenile 1 ($G = 22.876$, $p < 0.001$) in postures overall during resting. By postural modes, there were significant differences between Adults vs. Juveniles 2 by lie ($G = 8.254$, $p < 0.05$), and Adults vs. Juveniles 1 by cling ($G = 15.171$, $p < 0.001$) (Table 7.16).

Table 7.15. Postural profiles during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Sit	1,250	84.35%	575	82.73%	361	81.31%	68	81.93%	n.s.
Stand	159	10.73%	50	7.19%	35	7.88%	7	8.43%	n.s.
Lie	27	1.82%	28	4.03%	13	2.93%	2	2.41%	n.s.
Cling	25	1.69%	17	2.45%	24	5.41%	5	6.02%	***
Other posture	21	1.42%	25	3.60%	11	2.48%	1	1.20%	n.s.
Total	*1,482*	*100.00%*	*695*	*100.00%*	*444*	*100.00%*	*83*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and postural modes during resting after comparisons using Bonferroni correction. n.s.: not significant, *** $p < 0.001$. Overall ages: $G = 45.821$ ***.

Table 7.16. G-tests of age-based differences in postural behaviors during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Sit	0.080 n.s.	0.207 n.s.	0.030 n.s.	0.037 n.s.	0.003 n.s.	0.002 n.s.
Stand	5.944 n.s.	2.653 n.s.	0.381 n.s.	0.159 n.s.	0.138 n.s.	0.024 n.s.
Lie	8.254 *	1.815 n.s.	0.132 n.s.	0.905 n.s.	0.555 n.s.	0.067 n.s.
Cling	1.331 n.s.	15.171 ***	4.916 n.s.	6.150 n.s.	2.541 n.s.	0.045 n.s.
Other posture	9.600 n.s.	2.067 n.s.	0.026 n.s.	1.077 n.s.	1.598 n.s.	0.572 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Overall age classes: G(Adult vs. Juvenile 2) = 26.288 ***, G(Adult vs. Juvenile 1) = 22.876 ***, G(Adult vs. Infants) = 5.693 n.s., G(Juveniles 2 vs.1) = 8.664 n.s., G(Juveniles 2 vs. Infants) = 5.000 n.s., G(Juvenile 1 vs. Infants) = 0.729 n.s.

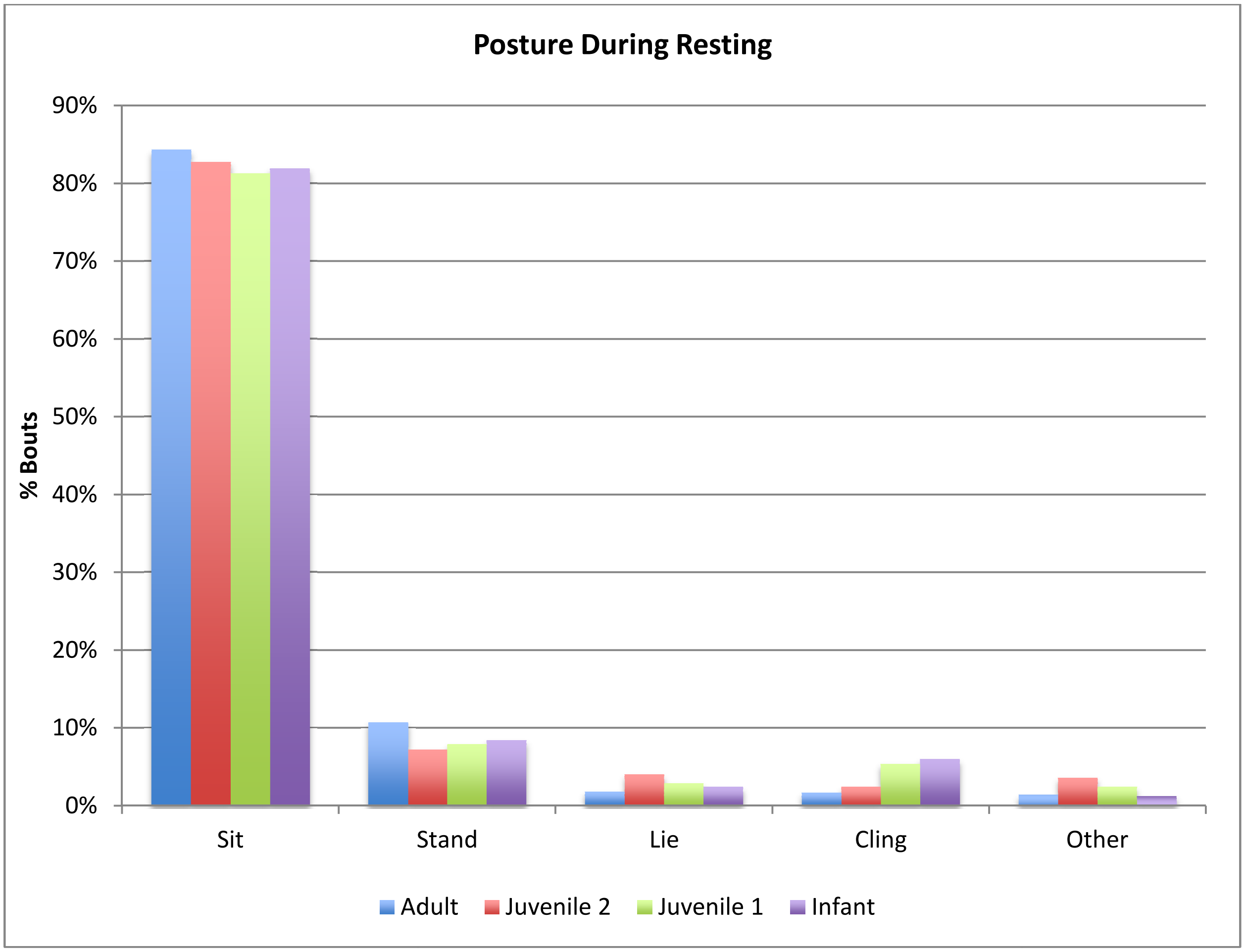

Figure 7.8. Frequencies of postural behavior during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

During resting, single supports were used most frequently by all age classes, and combined, multi, and networked supports were rarely used. There were no significant age-based differences in using support number overall (G = 4.912, n.s.), and by each support number use (Table 7.17; Figure 7.9).

Branches and boughs were the most commonly used support types by all ages during resting. There were significant differences between all ages and support size overall (G = 78.203, $p < 0.001$), and by twigs (G = 55.623, $p < 0.001$) (Table 7.17; Figure 7.9). All age classes differed in use of support size overall, by twigs (Tables 7.17-18).

There were significant differences of overall ages and support orientation use (G = 57.665, $p < 0.001$). Horizontal and oblique supports were used most frequent during resting, followed by vertical, terminal and forked supports. By types of support orientation, there were significant difference between ages by vertical supports (G = 12.075, $p < 0.05$) and terminal supports (G = 24.846, $p < 0.001$) ((Table 7.16; Figure 7.9). Significant interclass differences were seen for Adults vs. Juveniles, and Juveniles 2 vs. 1 (Table 7.18).

There were significant differences of overall ages and support flexibility during resting (G = 10.328, $p < 0.05$). Stable supports were used more frequently than flexible supports by all ages (Table 7.17; Figure 7.9). There were only significant differences between Adults vs. Juveniles 2 (G = 7.645, $p < 0.01$), and Juveniles 2 vs. 1 (G = 5.050, $p < 0.05$) in use of support flexibility. However, there were no significant differences of overall ages and age classes by either stable or flexible supports (Table 7.18).

Table 7.17. Support use during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Support number:									
Single	1,357	91.57%	631	90.79%	405	91.22%	76	91.57%	n.s.
Combined	100	6.75%	51	7.34%	31	6.98%	6	7.23%	n.s.
Multi	15	1.01%	11	1.58%	4	0.90%	1	1.20%	n.s.
Network	10	0.67%	2	0.29%	4	0.90%	-	-	n.s.
Subtotal	*1,482*	*100.00%*	*695*	*100.00%*	*444*	*100.00%*	*83*	*100.00%*	
Support size:									
Trunk	13	0.88%	4	0.58%	10	2.25%	-	-	n.s.
Bough	324	21.86%	127	18.27%	90	20.27%	10	12.05%	n.s.
Branch	1,114	75.17%	529	76.12%	312	70.27%	55	66.27%	n.s.
Twig	24	1.62%	30	4.32%	27	6.08%	17	20.48%	***
Liana	7	0.47%	5	0.72%	5	1.13%	1	1.20%	n.s.
Subtotal	*1,482*	*100.00%*	*695*	*100.00%*	*444*	*100.00%*	*83*	*100.00%*	
Support orientation:									
Horizontal	833	56.21%	331	47.63%	216	48.65%	46	55.42%	n.s.
Oblique	529	35.70%	280	40.29%	153	34.46%	29	34.94%	n.s.
Vertical	33	2.23%	18	2.59%	24	5.41%	5	6.02%	*
Terminal	13	0.88%	13	1.87%	22	4.95%	1	1.20%	***
Fork	74	4.99%	53	7.63%	29	6.53%	2	2.41%	n.s.
Subtotal	*1,482*	*100.00%*	*695*	*100.00%*	*444*	*100.00%*	*83*	*100.00%*	
Support flexibility:									
Flexible	531	35.83%	292	42.01%	157	35.36%	37	44.58%	n.s.
Stable	951	64.17%	403	57.99%	287	64.64%	46	55.42%	n.s.
Subtotal	*1,482*	*100.00%*	*695*	*100.00%*	*444*	*100.00%*	*83*	*100.00%*	

Note. The last column represents significance of age-based differences in support use during resting after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Ages vs. support use: G(number) = 4.912 n.s., G(size) = 78.203 ***, G(orientation) = 57.665 ***, G(flexibility) = 10.328 *.

Table 7.18. G-tests of age-based differences in support use during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Support number:	**2.942 n.s.**	**0.304 n.s.**	**1.143 n.s.**	**2.935 n.s.**	**0.531 n.s.**	**1.365 n.s.**
Single	0.016 n.s.	0.002 n.s.	0.000 n.s.	0.003 n.s.	0.003 n.s.	1.435 n.s.
Combined	0.220 n.s.	0.026 n.s.	0.025 n.s.	0.045 n.s.	0.001 n.s.	0.006 n.s.
Multi	1.215 n.s.	0.043 n.s.	0.027 n.s.	0.995 n.s.	0.073 n.s.	0.063 n.s.
Network	1.438 n.s.	0.227 n.s.	1.086 n.s.	1.864 n.s.	0.451 n.s.	1.442 n.s.
Support size:	**16.922 ****	**29.532 *****	**53.899 *****	**10.015 ***	**25.250 *****	**19.787 *****
Trunk	0.578 n.s.	4.605 n.s.	1.411 n.s.	5.967 n.s.	0.900 n.s.	3.393 n.s.
Bough	2.502 n.s.	0.337 n.s.	3.539 n.s.	0.472 n.s.	1.565 n.s.	2.394 n.s.
Branch	0.032 n.s.	0.647 n.s.	0.503 n.s.	0.727 n.s.	0.576 n.s.	0.097 n.s.
Twig	12.439 **	20.635 ***	44.242 ***	1.571 n.s.	19.585 ***	12.094 **
Liana	0.498 n.s.	2.027 n.s.	0.604 n.s.	0.493 n.s.	0.195 n.s.	0.004 n.s.
Support orientation:	**18.578 *****	**40.606 *****	**4.794 n.s.**	**16.721 ****	**7.733 n.s.**	**6.191 n.s.**
Horizontal	4.367 n.s.	2.404 n.s.	0.006 n.s.	0.040 n.s.	0.594 n.s.	0.414 n.s.
Oblique	1.923 n.s.	0.110 n.s.	0.009 n.s.	1.782 n.s.	0.401 n.s.	0.003 n.s.
Vertical	0.256 n.s.	9.804 n.s.	3.262 n.s.	5.433 n.s.	2.271 n.s.	0.045 n.s.
Terminal	3.595 n.s.	24.644 ***	0.085 n.s.	7.866 *	0.201 n.s.	2.915 n.s.
Fork	5.064 n.s.	1.366 n.s.	1.265 n.s.	0.426 n.s.	3.536 n.s.	2.389 n.s.
Support flexibility:	**7.645 ****	**0.033 n.s.**	**2.536 n.s.**	**5.050 ***	**0.199 n.s.**	**2.505 n.s.**
Flexible	3.393 n.s.	0.016 n.s.	1.117 n.s.	2.221 n.s.	0.079 n.s.	1.103 n.s.
Stable	1.825 n.s.	0.007 n.s.	0.612 n.s.	1.220 n.s.	0.054 n.s.	0.605 n.s.

Note. The last column represents significance of age-based differences in support use during resting after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

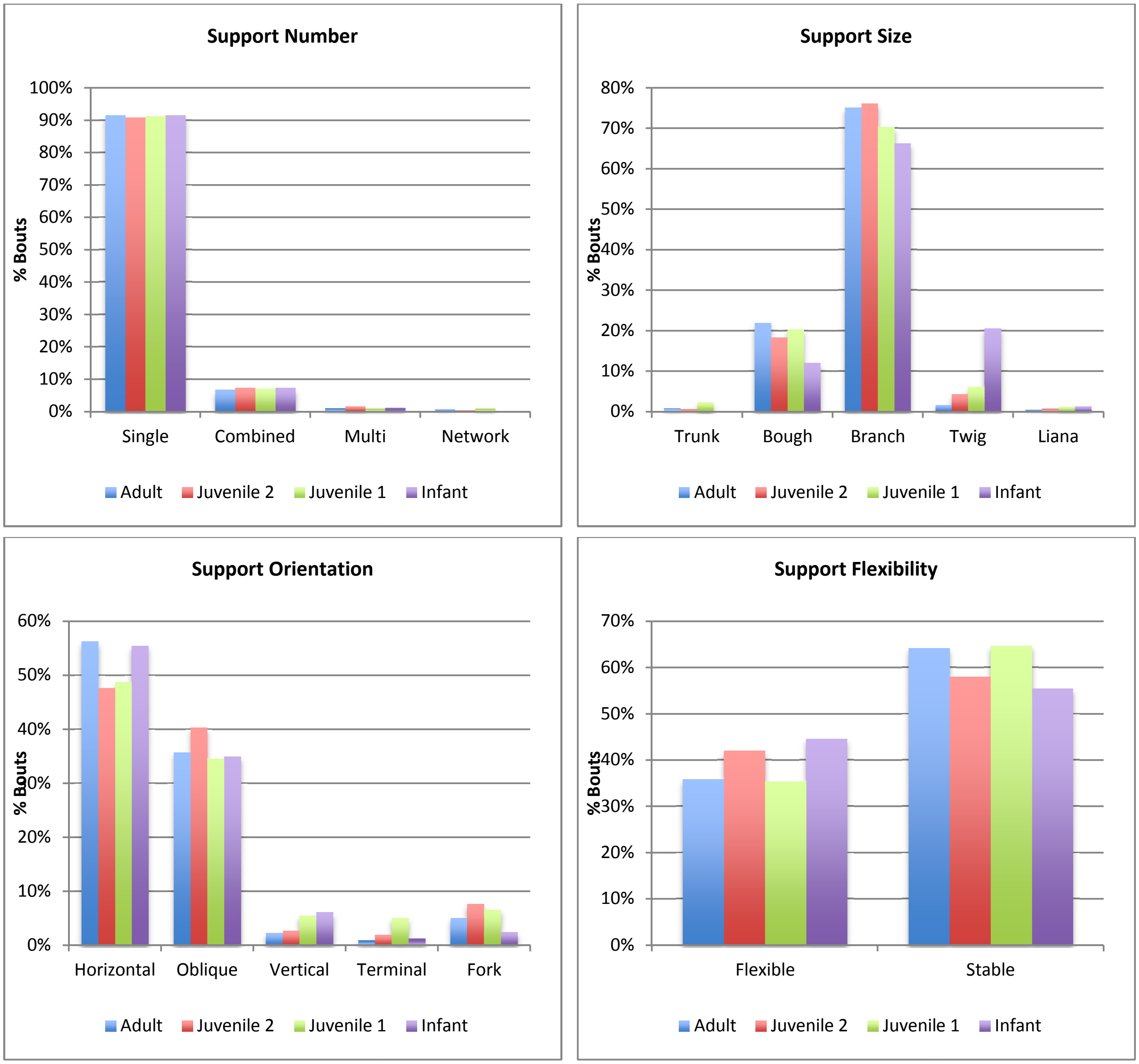

Figure 7.9. Frequencies of support use during resting by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

7.3.5. Age-based Differences During Displaying and Social Behaviors

All infant, juvenile and adult *R. avunculus* used postural modes including sit, stand, lie, cling and other during displaying and social. There were significant differences between ages in displaying and social behaviors overall (G = 24.525, $p < 0.05$). Sit was used most frequently (A: 68.94%; J2: 53.33%; J1: 65.00%; I: 70.21%), followed stand (A: 20.50%; J2: 30.679%; J1: 11.67%; I: 10.64%), lie (A: 6.83%; J2: 5.33%; J1: 8.33%; I: 8.51%), cling (A: 1.24%; J2: 4.00%; J1: 6.67%) and other posture (A: 2.48%; J2: 6.67%; J1: 8.33%; I: 10.64%) (Table 7.19; Figure 7.10). There were no significant differences by age classes during displaying and social behaviors (Table 7.20).

Table 7.19. Postural profiles during displaying and social behaviors by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Sit	111	68.94%	40	53.33%	39	65.00%	33	70.21%	n.s.
Stand	33	20.50%	23	30.67%	7	11.67%	5	10.64%	n.s.
Lie	11	6.83%	4	5.33%	5	8.33%	4	8.51%	n.s.
Cling	2	1.24%	3	4.00%	4	6.67%	-	-	n.s.
Other posture	4	2.48%	5	6.67%	5	8.33%	5	10.64%	n.s.
Total	*161*	*100.00%*	*75*	*100.00%*	*60*	*100.00%*	*47*	*100.00%*	

Note. The last column represents significance of differences between frequencies of ages and postural modes during displaying and social behaviors after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$. Overall ages: G = 24.525 *.

Table 7.20. G-tests of age-based differences in postural behaviors during displaying and social behaviors by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Sit	1.244 n.s.	0.060 n.s.	0.004 n.s.	0.485 n.s.	0.840 n.s.	0.063 n.s.
Stand	1.711 n.s.	1.769 n.s.	1.882 n.s.	4.804 n.s.	4.687 n.s.	0.022 n.s.
Lie	0.176 n.s.	0.123 n.s.	0.127 n.s.	0.418 n.s.	0.406 n.s.	0.001 n.s.
Cling	1.640 n.s.	3.935 n.s.	1.019 n.s.	0.431 n.s.	2.874 n.s.	4.515 n.s.
Other posture	2.072 n.s.	3.064 n.s.	4.329 n.s.	0.116 n.s.	0.499 n.s.	0.136 n.s.

Note. Significance of differences after comparisons using Bonferroni correction. n.s.: not significant. Overall age classes: G(Adult vs. Juvenile 2) = 8.171 n.s., G(Adult vs. Juvenile 1) = 9.561 *, G(Adult vs. Infants) = 7.913 n.s., G(Juveniles 2 vs.1) = 7.590 n.s., G(Juveniles 2 vs. Infants) = 10.887 *, G(Juvenile 1 vs. Infants) = 4.909 n.s.

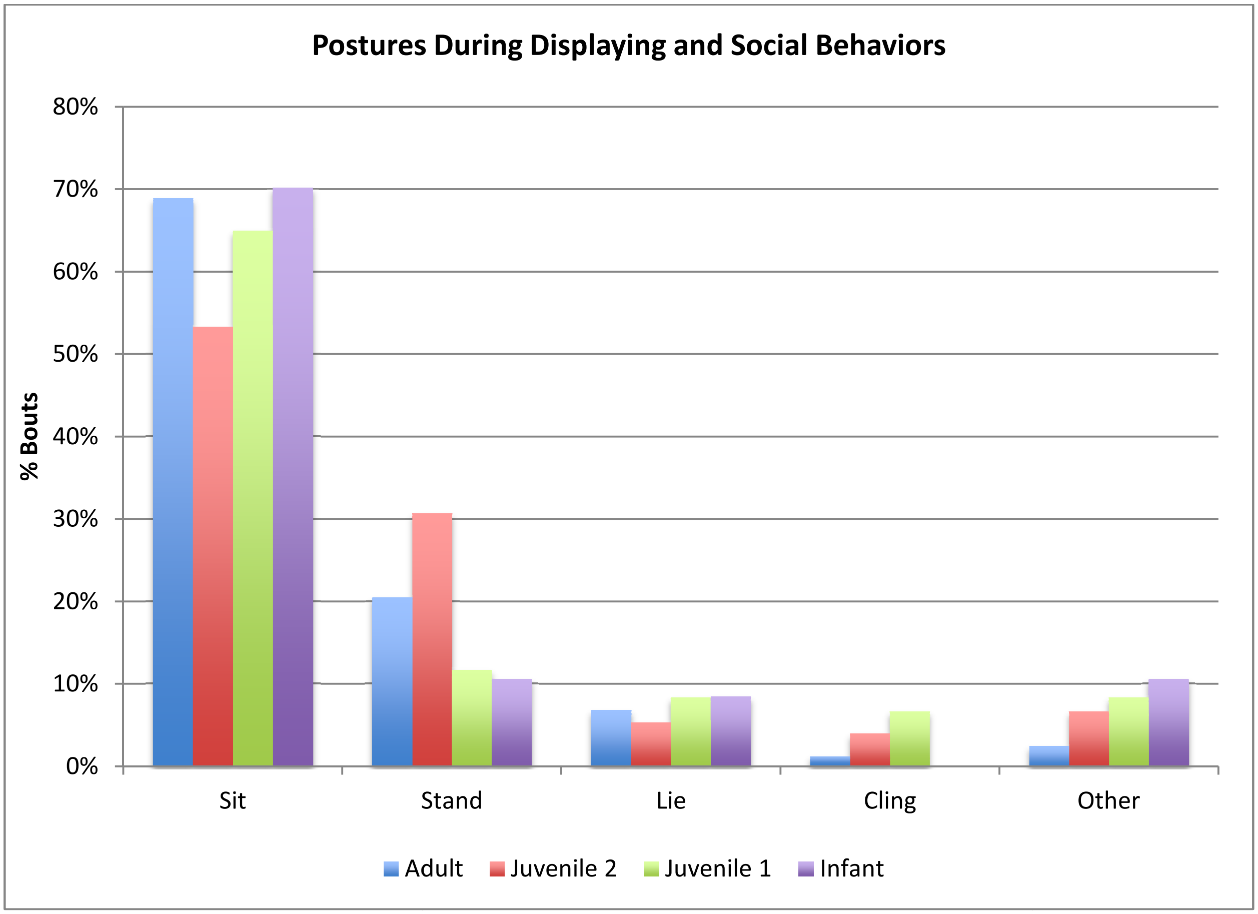

Figure 7.10. Frequencies of postural behaviors during displaying and social behaviors by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

Single supports were used most frequently by all ages during displaying and social behavior (A: 90.06%; J2: 97.33%; J1: 95.00%; I: 85.11), followed by combined supports (A: 8.70%; J2: 2.67%; I1: 5.00%; I: 7.89%). Only adults very seldom used multi and network supports (Table 7.21; Figure 7.11). There were no significant differences in use of support number by age classes (Table 7.22).

Branches and boughs were used most frequently by all ages. Trunks, twigs, and lianas were used occasional (Table 7. 21; Figure 7. 11). There were significant differences between age classes of Adults vs. Infants (26.198, $p < 0.001$), Juveniles 2 vs. Infants (30.142, $p < 0.001$), and Juveniles 1 vs. Infants (21.754, $p < 0.001$) in use of support size overall, and by twigs (Table 7.22).

There were significant differences for all ages in use of support orientation during displaying and social behaviors ($G = 23.386$, $p < 0.05$). All ages used horizontal and oblique supports most frequently; infants used horizontal support more and oblique supports less frequently than adults and juveniles (Table 7.21; Figure 7.11). There were only significant differences in support orientation overall between Adults vs. Infants ($G = 13.507$, $p < 0.01$), and Juveniles 2 vs. Infants ($G = 15.918$, $p < 0.01$) (Table 7.22).

Stable supports were used more frequently than flexible supports during displaying and social behaviors. There were no significant differences of overall ages, and age classes in use of support flexibility (Tables 7.21-22; Figure 7.11).

Table 7.21. Support use during displaying and social behaviors by *R. avunculus* in Khau Ca Forest

	Adult		Juvenile 2		Juvenile 1		Infant		
	n	%	n	%	n	%	n	%	
Support number:									
Single	145	90.06%	73	97.33%	57	95.00%	40	85.11%	n.s.
Combined	14	8.70%	2	2.67%	3	5.00%	7	14.89%	n.s.
Multi	1	0.62%	-	-	-	-	-	-	n.s.
Network	1	0.62%	-	-	-	-	-	-	n.s.
Subtotal	*161*	*100.00%*	*75*	*100.00%*	*60*	*100.00%*	*47*	*100.00%*	
Support size:									
Trunk	2	1.24%	-	-	1	1.67%	-	-	n.s.
Bough	43	26.71%	16	21.33%	10	16.67%	9	19.15%	n.s.
Branch	111	68.94%	59	78.67%	48	80.00%	24	51.06%	n.s.
Twig	4	2.48%	-	-	1	1.67%	12	25.53%	***
Liana	1	0.62%	-	-	-	-	2	4.26%	n.s.
Subtotal	*161*	*100.00%*	*75*	*100.00%*	*60*	*100.00%*	*47*	*100.00%*	
Support orientation:									
Horizontal	82	50.93%	33	44.00%	30	50.00%	32	68.09%	n.s.
Oblique	67	41.61%	32	42.67%	22	36.67%	10	21.28%	n.s.
Vertical	1	0.62%	3	4.00%	3	5.00%	1	2.13%	n.s.
Terminal	1	0.62%	-	-	1	1.67%	3	6.38%	n.s.
Fork	10	6.21%	7	9.33%	4	6.67%	1	2.13%	n.s.
Subtotal	*161*	*100.00%*	*75*	*100.00%*	*60*	*100.00%*	*47*	*100.00%*	
Support flexibility:									
Flexible	54	33.54%	27	36.00%	19	31.67%	22	46.81%	n.s.
Stable	107	66.46%	48	64.00%	41	68.33%	25	53.19%	n.s.
Subtotal	*161*	*100.00%*	*75*	*100.00%*	*60*	*100.00%*	*47*	*100.00%*	

Note. The last column represents significance of age-based differences in support use displaying and social behaviors after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Ages vs. support use: G(number) = 10.249 n.s., G(size) = 46.715 ***, G(orientation) = 23.386 *, G(flexibility) = 3.201 n.s.

Table 7.22. G-tests of age-based differences in support use during displaying and social behaviors by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

	Adult vs. Juvenile 2	Adult vs. Juvenile 1	Adult vs. Infant	Juvenile 2 vs. Juvenile 1	Juvenile 2 vs. Infant	Juvenile 1 vs. Infant
Support number:	**5.057 n.s.**	**2.231 n.s.**	**2.388 n.s.**	**0.505 n.s.**	**6.237 n.s.**	**3.057 n.s.**
Single	0.150 n.s.	0.060 n.s.	0.054 n.s.	0.001 n.s.	0.246 n.s.	0.150 n.s.
Combined	3.061 n.s.	0.792 n.s.	1.136 n.s.	0.469 n.s.	5.367 n.s.	2.536 n.s.
Multi	0.763 n.s.	0.632 n.s.	0.511 n.s.	-	-	-
Network	0.763 n.s.	0.632 n.s.	0.511 n.s.	-	-	-
Support size:	**6.623 n.s.**	**3.535 n.s.**	**26.198 *****	**3.632 n.s.**	**30.142 *****	**21.754 *****
Trunk	1.522 n.s.	0.055 n.s.	1.019 n.s.	1.613 n.s.	-	1.150 n.s.
Bough	0.490 n.s.	1.622 n.s.	0.716 n.s.	0.320 n.s.	0.056 n.s.	0.077 n.s.
Branch	0.382 n.s.	0.419 n.s.	1.175 n.s.	0.004 n.s.	2.037 n.s.	2.035 n.s.
Twig	3.028 n.s.	0.135 n.s.	18.022 ***	1.613 n.s.	21.204 ***	12.521 **
Liana	0.763 n.s.	0.632 n.s.	2.596 n.s.	-	3.764 n.s.	3.244 n.s.
Support orientation:	**5.099 n.s.**	**4.719 n.s.**	**13.507 ****	**2.550 n.s.**	**15.918 ****	**7.114 n.s.**
Horizontal	0.348 n.s.	0.005 n.s.	1.177 n.s.	0.174 n.s.	1.984 n.s.	0.931 n.s.
Oblique	0.009 n.s.	0.194 n.s.	3.474 n.s.	0.216 n.s.	3.113 n.s.	1.674 n.s.
Vertical	3.078 n.s.	3.876 n.s.	0.706 n.s.	0.071 n.s.	0.318 n.s.	0.597 n.s.
Terminal	0.763 n.s.	0.464 n.s.	4.821 n.s.	1.613 n.s.	5.609 n.s.	1.538 n.s.
Fork	0.616 n.s.	0.013 n.s.	1.337 n.s.	0.274 n.s.	2.549 n.s.	1.217 n.s.
Support flexibility:	**0.137 n.s.**	**0.070 n.s.**	**2.704 n.s.**	**0.279 n.s.**	**1.399 n.s.**	**2.554 n.s.**
Flexible	0.066 n.s.	0.035 n.s.	1.191 n.s.	0.138 n.s.	0.586 n.s.	1.127 n.s.
Stable	0.029 n.s.	0.014 n.s.	0.654 n.s.	0.057 n.s.	0.361 n.s.	0.617 n.s.

Note. The last column represents significance of age-based differences in support use displaying and social behaviors after comparisons using Bonferroni correction. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

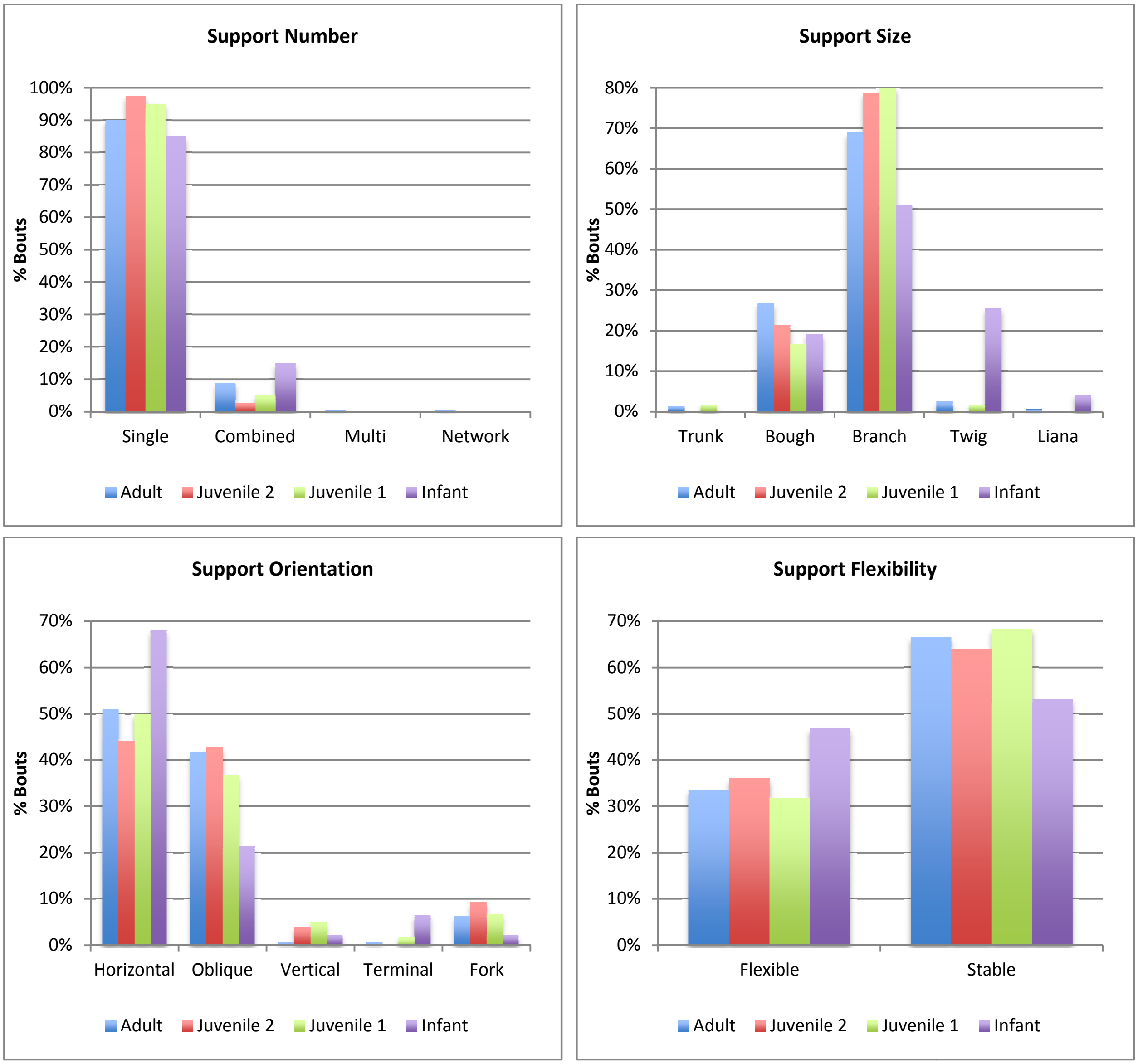

Figure 7.11. Frequencies of support use during displaying and social behaviors by infant, juvenile and adult *R. avunculus* in Khau Ca Forest

7.4. Discussion

The aim of this chapter was to examine the age-based differences in positional behavior and support use of *R. avunculus*. The results indicate that there were significant age-based differences in activity patterns, positional behaviors and support use for *R. avunculus* in Khau Ca Forest. These results reject Hypothesis 7.1 that predicted there was no significant difference in positional behavior and substrate use between adult and immature.

During maintenance activities, all ages were not significantly different in travel and displaying, but significantly different in foraging, feeding, resting and social behaviors. Adults and Juveniles were not significantly different in all maintenance activities. Juveniles 1 and 2 just differed in social behaviors. Adults and Juveniles significantly differed from Infants in in foraging, feeding, resting and social behaviors.

For locomotion, I hypothesized that larger-bodied adult *R. avunculus* would more frequently use suspensory behavior and climbing, and less frequently leap (Hypothesis 7.2); and more frequently use larger and more stable supports than smaller-bodied immature individuals (i.e., juveniles and infants) (Hypothesis 7.3) (Fleagle and Mittermeier, 1980). However, I found only frequencies of leaping and climbing support this hypothesis, although these differences were not statistically significant. Although there were significantly age-based differences in arm-swing (suspensory behavior), these results were not as predicted. Previous primate studies also showed there were age-based differences in locomotor behaviors, however, these differences were not consistent with suggestions of Fleagle and Mittermeier (1980) (Table 7.23). For examples Bezanson (2006a) reported that Adult and Infant 2 mantled howlers (*Alouatta palliata*) used leap and climb less frequently than Juveniles 1 and 2. Infant white-faced capuchins (*Cebus capucinus*) used leap and climb less frequently than juveniles and adults; while Juveniles 1 used leap and climb more frequently than older animals (Juveniles 2 and Adults), but there are relatively no differences in leaping and climbing by Juveniles 2 and Adults. Fan *et al.* (2013) reported that leaping frequencies increased by age in Cao Vit gibbons (*Nomascus nasutus*) but climbing frequencies decreased, and brachiation by adults was less frequent than juveniles and infants. Doran (1992) found both pygmy chimpanzees (*Pan panicus*) and common chimpanzees (*P. troglodytes*) significantly changed their locomotor patterns and that their frequencies of suspensory behavior decreased with age. Finally, Lawler (2006) observed no differences in locomotor behaviors between juvenile and adult Verreaux's sifaka (*Propithecus verreauxi verreauxi*).

In this study, infant, juvenile and adult *R. avunculus* significantly differed in postural modes during resting, feeding, displaying and social behaviors. The frequency of sitting increased with age during resting and feeding, but was not significantly different. Standing was slightly different in all ages; adults and infants were relatively similar, and more frequent than juveniles. There were relatively few previous studies on age-based differences in postures of primates. Bezanson (2006b) found that all ages of mantled howlers and white-faced capuchins differed in postures during resting, feeding/foraging and social behaviors; however, these age-based differences were not statistically significant. Prates and Bicca-Marques (2008) reported significantly age-based differences during resting and feeding by black-and-gold howlers (*Alouatta caraya*), however, there were no numerical data presented in their publication

All age classes of *R. avunculus* significantly differed in support use. Nevertheless, I found only results on use of support size support Hypothesis 7.3 that larger-sized older *R. avunculus* tended to use larger support more than smaller-sized younger animals. My data showed that older *R. avunculus* tended to use flexible supports more frequently than did younger animals; an observation that did not support Hypothesis 7.3. Similarly, Bezanson (2006b) and Fan *et al.* (2013) also found the same trends in use of support size in mantled howlers, white-faced capuchins, and Cao Vit gibbons (Table 7.24).

Table 7.23. Age-based differences in locomotion by primates

		Quadrupedalism						
		Walk	Run	Leap	Climb	Drop	Suspensory	Other
Alouatta palliata[1]	Adult	77.30%	1.80%	2.40%	5.90%	1.30%	88.70%	11.30%
	Juvenile 2	62.40%	5.70%	7.00%	9.20%	1.40%	85.70%	14.30%
	Juvenile 1	64.70%	7.90%	6.10%	10.80%	< 1.0%	89.50%	10.50%
	Infant 2	18.40%	-	3.40%	1.50%	-	23.30%	76.70%
	Infant 1	5.30%	-	-	-	-	5.30%	94.70%
Cebus capucinus[1]	Adult	76.60%	4.30%	10.30%	6.80%	< 1.0%	98.00%	< 2.0%
	Juvenile 2	66.70%	11.70%	10.80%	6.40%	< 1.0%	95.60%	< 4.0%
	Juvenile 1	55.90%	17.20%	15.50%	9.20%	< 1.0%	97.80%	< 2.0%
	Infant 2	27.30%	5.40%	3.10%	6.20%	< 1.0%	42.00%	58.00%
	Infant 1	3.40%	-	-	4.50%	-	7.90%	92.10%
Rhinopithecus avunculus[2]	Adult	54.70%		14.32%	13.24%	10.25%	5.69%	1.80%
	Juvenile 2	48.54%		16.26%	12.45%	11.18%	9.53%	2.03%
	Juvenile 1	51.70%		15.09%	13.96%	11.32%	3.96%	3.96%
	Infant	46.75%		18.93%	11.24%	10.65%	9.47%	2.96%
Nomascus nasutus[3]	Adult	1.19%	0.01%	8.60%	21.10%	-	54.77%	14.35%
	Juvenile 2	1.00%	-	9.20%	16.90%	-	65.70%	7.20%
	Juvenile 1	0.60%	-	6.70%	21.20%	-	62.80%	8.70%
	Infant	0.70%	-	2.80%	28.20%	-	63.70%	4.50%

Note. [1] Bezanson (2006a), [2] In this study, [3] Fan *et al.* (2013).

Table 7.24. Age-based differences in support use by primates

		Trunk	Bough	Branch	Twig	Liana	Other
Alouatta palliata[1]	Adult	-	0.70%	44.80%	53.40	-	1.10%
	Juvenile 2	-	14.20%	46.00%	37.70	-	2.10%
	Juvenile 1	-	4.40%	30.70%	64.20	-	0.70%
	Infant 2	-	5.90%	31.50%	61.30	-	1.30%
Cebus capucinus[1]	Adult	-	16.60%	43.50%	38.10	-	1.90%
	Juvenile 2	-	14.40%	46.90%	34.80	-	3.90%
	Juvenile 1	-	12.80%	40.40%	43.80	-	3.00%
	Infant 2	-	31.10%	30.80%	34.50	-	3.60%
Rhinopithecus avunculus[2]	Adult	1.77%	19.33%	72.54%	5.36%	1.00%	-
	Juvenile 2	0.66%	15.19%	75.99%	6.66%	1.50%	-
	Juvenile 1	2.28%	16.97%	69.43%	9.12%	2.19%	-
	Infant	0.28%	11.68%	56.41%	29.34%	2.28%	-
Nomascus nasutus[3]	Adult male	-	3.54%	63.52	23.17%	9.77%	-
	Juvenile 2	-	2.00%	64.20	24.20%	9.60%	-
	Juvenile 1	-	1.40%	52.80	33.20%	12.60%	-
	Infant	-	0.40%	53.80	32.10%	13.60%	-

Note. [1] Bezanson (2006b), [2] In this study, [3] Fan *et al.* (2013).

Thus, this study showed that age-based differences in body size influenced positional behavior and support use of *R. avunculus,* but not in a way consistent with predictions suggested by Fleagle and Mittermeier (1980) and reported by Bezanson (2006a, 2006b), Fan *et al.* (2013), Lawler (2006), and Prates and Bicca-Marques (2008). In addition, ontogeny is likely complex in ways differing from interspecific variation. To further understand effects of age-based differences in positional behavior, Bezanson and Morbeck (2013) suggested that this "…requires additional research at several levels including social behaviors, body mass, growth, physiology, anatomy, skeletal kinematics, and loading conditions" (p. 451).

Summary

- There were significant age-based differences during resting and social behaviors; and no significant differences during traveling, foraging and displaying for *R. avunculus*.
- Quadrupedalism was the most frequent locomotor mode for all ages, followed by leap, climb, drop, arm-swing and other locomotion. Sit was the most common postural mode for all ages, followed by stand, lie, cling and other postures.
- There were significant age-based differences in positional behavior and support use of *R. avunculus* during maintenance activities. Larger-bodied adults climbed more frequently, and leap less frequently than smaller-bodied juveniles and infants during travel. The frequency of sitting was increased with increasing ages during resting and feeding. Larger-bodied adults tended to use larger support and flexible supports more than smaller-bodied juveniles and infants.
- Age-related differences in body size influenced the positional behavior and support use of *R. avunculus*, but no consistent with predictions based on the work of Fleagle and Mittermeier (1980).

CHAPTER VIII

INFLUENCE OF SEASONAL CHANGES

8.1. Introduction

Seasonal changes affect diet, food availability and distribution, and activity patterns of primates living in tropical areas (e.g., Brockman and van Schaik, 2005; Hoang Minh Duc *et al.*, 2009; Lemelin and Schmitt, 2004; Li *et al.*, 2000; Li *et al.*, 2010; Li, 2006; Phiapalath *et al.*, 2011; Ren *et al.*, 2009a; Ren *et al.*, 2009b; Xiang and Sayers, 2009; Yiming, 2002; Zhang *et al.*, 2000). Seasonal changes would be expected to affect patterns of primate positional behavior (Garber, 2011). Studies of Dagosto (1995), Gebo and Chapman (1995a), Lemelin and Schmitt (2004), and Youlatos (1998b) found that a higher degree of variability in positional repertoire during feeding may be associated with seasonal changes in diet, foraging strategies, and availability and distribution of feeding sites. Dagosto (1995, p. 811) concluded that “locomotion during travel appears to be fairly conservative while differences during feeding contribute substantially to the overall differences observed.”

In this chapter, I analyze and compare quantitative data on the positional behavior and support use of *R. avunculus* in Khau Ca Forest, collected during two different seasons (wet/warm and dry/cool) in two successive years (2009, 2010). The object of this study is to determine if there are seasonal differences in the positional behavior of *R. avunculus* and if they are correlated with associated maintenance contexts and support preference resulting from temporal shifts in climate.

Hypothesis to test is the following:

<u>Hypothesis 8:</u> Because of living in a seasonal habitat, *R. avunculus* exhibits significant differences in positional behavior and support use by dry/cool and wet/warm seasons.

The question to be addressed in this chapter:

- Is there any seasonal variation in positional behavior, and if so, which locomotor and postural behaviors are most affected?

8.2. Methods

To determine the seasonal changes in Khau Ca region, I use temperature and rainfall data collected at the Ha Giang Meteorological Station for 2009 – 2010, and with special references from Nguyen Khanh Van *et al.* (2000) who analyzed climatological data in Vietnam for 50 years. In this study, I recognized two distinctive seasons of wet and hot (wet/warm) from June to August, and dry and cold season from December to February. The study site and its climatic conditions are described in detail Chapter IV.

Proportions calculated for positional behaviors and support use were based on the bout method of recording on focal animal (Fleagle, 1976; Doran, 1992) and, thus, represent the frequency of use of various behaviors. Details of behavioral collection protocol are presented in Chapter III. In this study, I used data on positional behavior and support use by *R. avunculus* in January, February and December of 2009 and 2010 for the dry/cool season dataset, and June – August of 2009 and 2010 for the wet/warm season dataset.

Following to Youlatos (1998b), I compared profiles for all postures and all locomotor behaviors and support use by *R. avunculus* between wet/warm and dry/cool seasons in Khau Ca Forest using the G-Tests of independence with the Bonferroni correction (MacDonald, 2008). All tests were two-tailed and performed using Microsoft Excel (see MacDonald, 2008).

8.3. Results

8.3.1. Maintenance Behavioral Contexts

Maintenance activities differed significantly between the seasons for *R. avunculus* in Khau Ca Forest (G = 96.895, $p < 0.001$). In the dry/cool season, forage, feed and social behaviors occurred more frequently [Dry/cool vs. wet/warm: G(forage) = 13.950, $p < 0.01$; G(feed) = 58.510, $p < 0.001$; G(social behaviors) = 6.227, n.s.]. In the wet/warm season, travel, rest and display occurred more frequently but there were no significant differences [Dry/cool vs. wet/warm: G(travel) = 1.495, n.s.; G(rest) = 4.297. n.s.; G (display) = 5.804, n.s.] (Table 8.1; Figure 8.1).

Table 8.1. Seasonal changes in maintenance activities by *R. avunculus* in Khau Ca Forest

	Dry/cool		Wet/warm		
	n	%	n	%	
Travel	686	42.48%	913	45.74%	n.s.
Forage	57	3.53%	31	1.55%	**
Rest	615	38.08%	865	43.34%	n.s.
Feed	155	9.60%	63	3.16%	***
Display	37	2.29%	74	3.71%	n.s.
Social behaviors	65	4.02%	50	2.51%	n.s.
Total	*1,615*	*100.00%*	*1,996*	*100.00%*	

Note. The last column represents significance of differences between the dry/cool and wet/warm seasons after comparisons using Bonferroni correction. n.s.: not significant, ** $p < 0.01$, *** $p < 0.001$. Overall maintenance activities: G = 96.895 ***

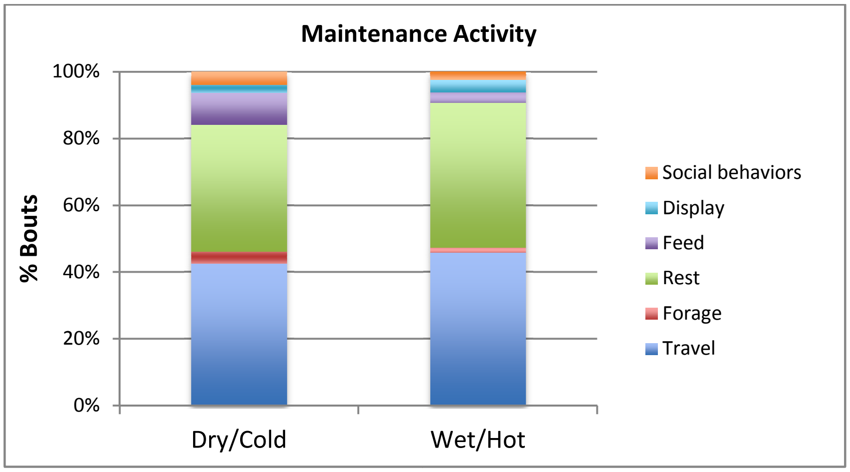

Figure 8.1. Frequencies of seasonal changes in maintenance activities by *R. avunculus* in Khau Ca Forest

8.3.2. Locomotion

Overall, there were significant differences in the frequency of locomotor modes between seasons ($G = 30.150$, $p < 0.001$). In the wet/warm season, *R. avunculus* used leap, climb and arm-swing more frequently, and used quadrupedalism and drop less frequently than in the dry/cool season; other locomotion was fairly similar in both seasons (Table 8.2; Figure 8.2). There was only significant difference between seasons by dropping ($G = 7.837$, $p < 0.05$) (Table 8.3).

Travel locomotion significantly differed between seasons ($G = 24.248$, $p < 0.001$). Quadrupedalism and drop were used more frequently in dry/cool season while leaping, climbing, arm-swinging and other locomotion were used more frequently in the wet/warm season (Table 8.2; Figure 8.2). Only drop was significantly different between seasons during travel (Table 8.3).

During foraging, *R. avunculus* used climb and arm-swing more frequently in the wet/warm season, and they used quadrupedalism, leap and drop more frequently in the dry/cool season (Table 8.2; Figure 8.2). However, there were no significant differences in locomotion between seasons (Table 8.3).

Table 8.2. Seasonal changes in locomotion by *R. avunculus* in Khau Ca Forest

	Forage				Travel				Overall locomotion			
	Dry/cool		Wet/warm		Dry/cool		Wet/warm		Dry/cool		Wet/warm	
	n	%	n	%	n	%	n	%	n	%	n	%
Quadrupedalism	44	77.19%	20	64.52%	397	57.87%	473	51.81%	441	59.35%	493	52.22%
Leap	1	1.75%	-	-	90	13.12%	154	16.87%	91	12.25%	154	16.31%
Climb	4	7.02%	6	19.35%	72	10.50%	129	14.13%	76	10.23%	135	14.30%
Arm-swing	2	3.51%	4	12.90%	33	4.81%	72	7.89%	35	4.71%	76	8.05%
Drop	6	10.53%	1	3.23%	83	12.10%	70	7.67%	89	11.98%	71	7.52%
Other locomotion	-	-	-	-	11	1.60%	15	1.64%	11	1.48%	15	1.59%
Total	*57*	*100.00%*	*31*	*100.00%*	*686*	*100.00%*	*913*	*100.00%*	*743*	*100.00%*	*944*	*100.00%*

Table 8.3. G-tests of seasonal differences in locomotion by *R. avunculus* in Khau Ca Forest

	Forage	Travel	Overall locomotion
Overall	**7.857, n.s.**	**24.248 *****	**30.150 *****
Quadrupedalism	0.264, n.s.	1.704, n.s.	2.442, n.s.
Leap	0.862, n.s.	3.18, n.s.	4.201, n.s.
Climb	2.263, n.s.	3.726, n.s.	4.996, n.s.
Arm-swing	2.281, n.s.	5.48, n.s.	6.843, n.s.
Drop	1.457, n.s.	7.236 *	7.873 *
Other locomotion	-	0.004, n.s.	0.031, n.s.

Note. n.s.: not significant, * $p < 0.05$, *** $p < 0.001$

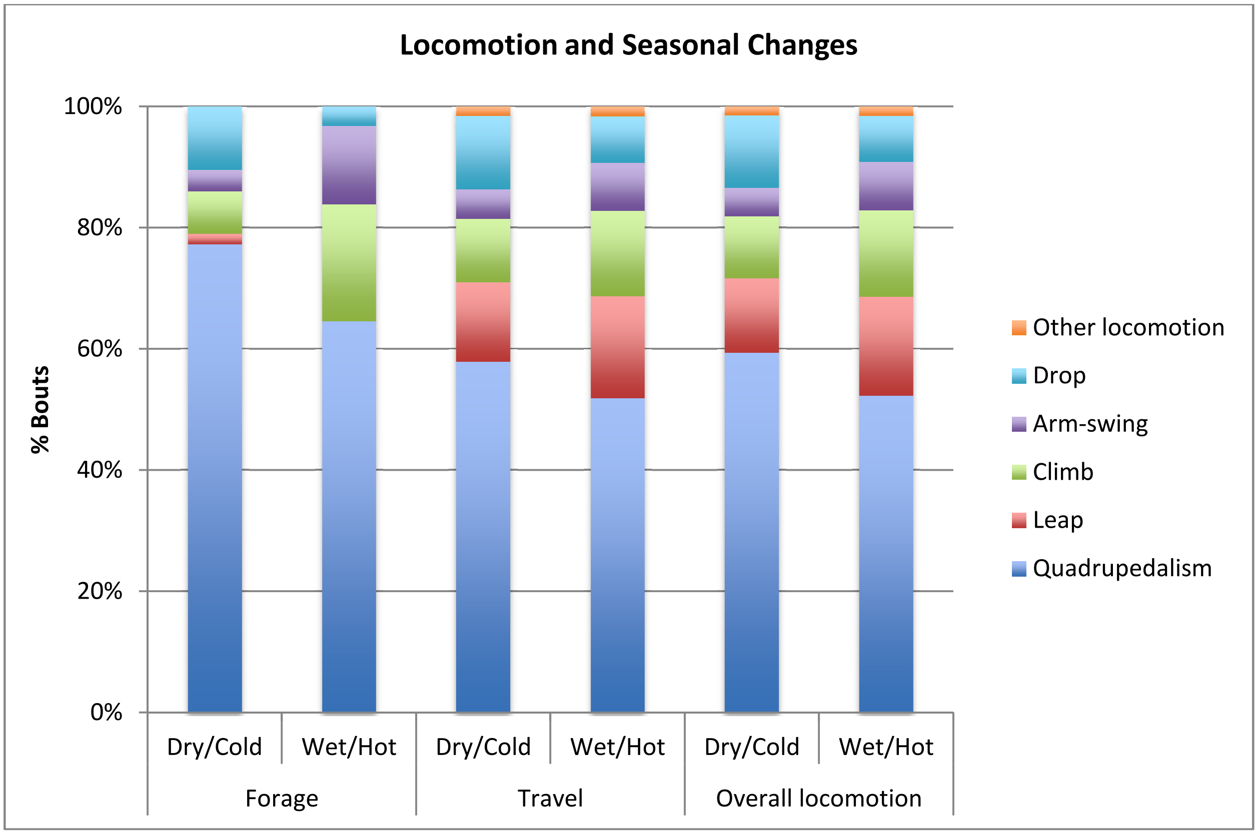

Figure 8.2. Frequencies of locomotion in the dry/cool and wet/warm seasons by *R. avunculus* in Khau Ca Forest

8.3.3. Posture

Overall, there were significant seasonal differences in postures by *R. avunculus* ($G = 24.237$, $p < 0.001$). Sit was used more frequently in the dry/cool season while stand, lie, cling and other posture were used more frequently in the wet/warm season, but there were no significant differences in these postures between seasons (Tables 8.4-5; Figure 8.3). The only significant difference between seasons, however, was in other postures ($G = 11.506$, $p < 0.001$). There were significantly seasonal differences in postural modes during resting ($G = 20.600$, $p < 0.001$), feeding ($G = 10.533$, $p < 0.05$) and displaying ($G = 12.670$, $p < 0.05$) (Table 8.6).

During resting and feeding in the dry/cool season, sit was used more frequently while resting and feeding, but less frequently while displaying and social behaviors than in the wet/warm season. Stand was used more frequently during resting and feeding, and less frequently during dispalying in the wet/warm season. Cling and other postures were rarely recorded and differed only slightly between seasons. Statistically, there were only significant seasonal differences by other postures during resting ($G = 7.763$, $p < 0.05$) and feeding ($G = 7.346$, $p < 0.05$) (Table 8.6).

Table 8.4. Seasonal changes in overall postures by *R. avunculus* in Khau Ca Forest

	Overall Postures				
	Dry/cool		Wet/warm		
	n	%	n	%	
Sit	750	86.01%	828	78.71%	n.s.
Stand	71	8.14%	117	11.12%	n.s
Lie	15	1.72%	35	3.33%	n.s
Cling	22	2.52%	27	2.57%	n.s
Other posture	14	1.61%	45	4.28%	***
Total	*872*	*100.00%*	*1,052*	*100.00%*	

Note. The last column represents significance of differences between the dry/cool and wet/warm seasons after comparisons using Bonferroni correction. n.s.: not significant, *** $p < 0.001$.
Overall seasons: G = 24.237 ***

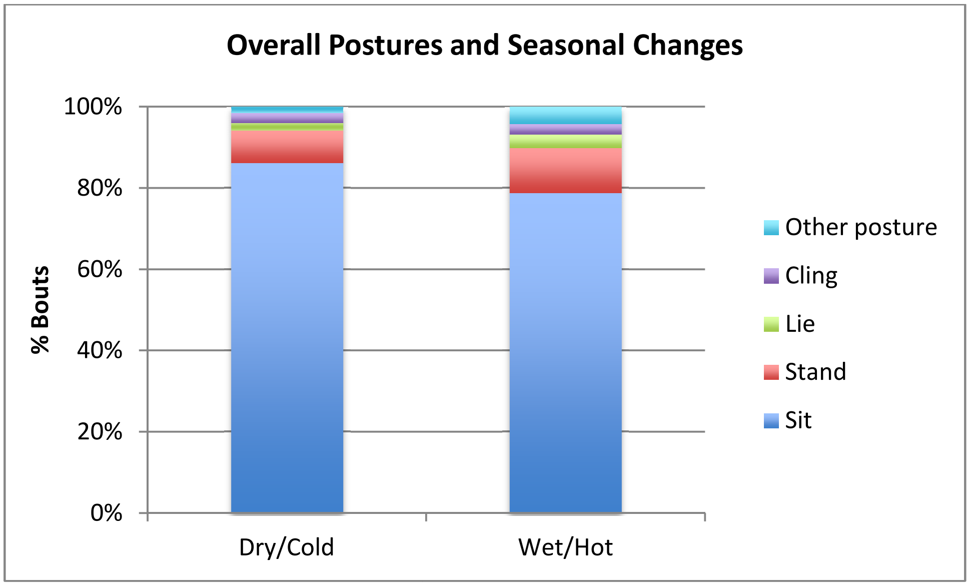

Figure 8.3. Frequencies of postures in the dry/cool and wet/warm seasons by *R. avunculus* in Khau Ca Forest

Table 8.5. Seasonal changes in postures during maintenance activities by *R. avunculus* in Khau Ca Forest

	Rest				Feed				Display				Social behaviors			
	Dry/cool		Wet/warm		Dry/cool		Wet/warm		Dry/cool		Wet/warm		Dry/cool		Wet/warm	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Sit	544	88.46%	701	81.04%	143	92.26%	50	79.37%	11	29.73%	36	48.65%	52	80.00%	41	82.00%
Stand	43	6.99%	88	10.17%	3	1.94%	2	3.17%	20	54.05%	27	36.49%	5	7.69%	-	-
Lie	8	1.30%	28	3.24%	-	-	-	-	2	5.41%	1	1.35%	5	7.69%	6	12.00%
Cling	15	2.44%	24	2.77%	2	1.29%	-	-	4	10.81%	3	4.05%	1	1.54%	-	-
Other posture	5	0.81%	24	2.77%	7	4.52%	11	17.46%	-	-	7	9.46%	2	3.08%	3	6.00%
Total	*615*	*100.00%*	*865*	*100.00%*	*155*	*100.00%*	*63*	*100.00%*	*37*	*100.00%*	*74*	*100.00%*	*65*	*100.00%*	*50*	*100.00%*

Table 8.6. G-tests of seasonal differences in postures during maintenance activities by *R. avunculus* in Khau Ca Forest

	Rest	Feed	Display	Social behaviors
Overall	**20.600 *****	**10.533 ***	**12.670 ***	**7.952, n.s.**
Sit	1.267, n.s.	0.461, n.s.	1.586, n.s.	0.008, n.s.
Stand	3.885, n.s.	0.275, n.s.	1.202, n.s.	5.545, n.s.
Lie	5.856, n.s.	-	1.347, n.s.	0.494, n.s.
Cling	0.151, n.s.	1.357, n.s.	1.556, n.s.	1.134, n.s.
Other posture	7.763 *	7.346 *	5.467, n.s.	0.526, n.s.

Note. n.s.: not significant, * p < 0.05. *** p < 0.001

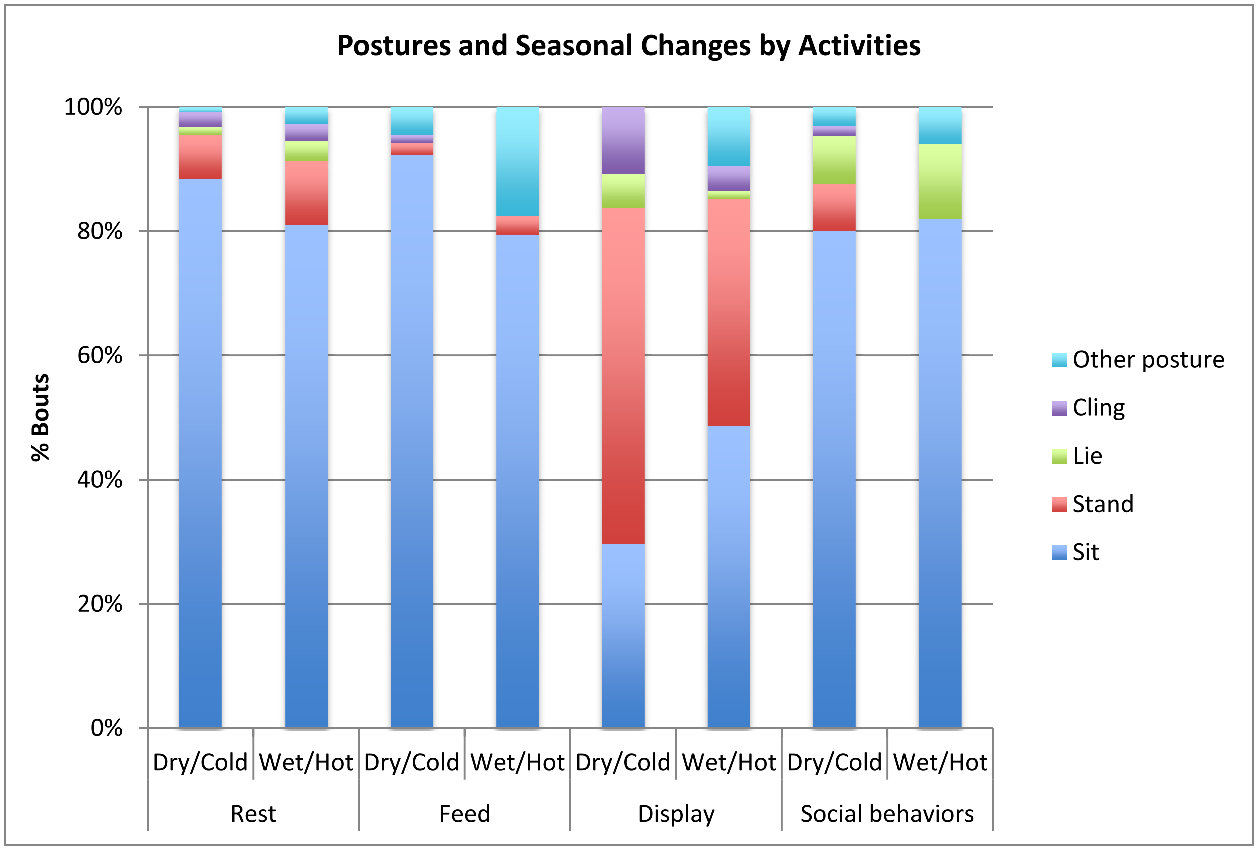

Figure 8.4. Frequencies of seasonal changes in postures by maintenance activities of *R. avunculus* in Khau Ca Forest

8.3.4. Support Use

There were significant seasonal differences in use of support number by overall positional modes (G = 18.246, $p < 0.001$), and locomotion (G = 13.572, $p < 0.01$). Single, multi and network supports were used more frequently in the wet/warm season, and combined supports were used more frequently in the dry/cool season. However, there was only significant seasonal difference by network supports by overall, and locomotion (Tables 8.7-8; Figure 8.5).

The use of support size was significantly different in locomotion (G = 15.763, $p < 0.01$) and postures (G = 30.361, $p < 0.001$) by seasons. Branches and lianas were used more frequently in the dry/cool season; trunks, boughs and twigs were used more frequently in the wet/warm season (Table 8.7; Figure 8.5). Trunk use differed significantly between seasons in overall positional modes but did not differ significantly for either locomotion or postures. Liana use differed significantly between seasons for both locomotion and postures (Table 8.8).

Horizontal supports were used more frequently during locomotion and postures in the dry/cool season; oblique, vertical, terminal and forked supports were used more frequently in the wet/warm season (Table 8.7); Figure 8.5. There were significant seasonal differences in use of support orientation by locomotion (G = 20.368, $p < 0.01$) and postures (G = 31.280, $p < 0.001$). *R. avunculus* use of horizontal supports differed significantly between seasons by overall positional behavior overall, but not for either locomotion or postures (Table 8.8).

R. avunculus used stable supports more frequently in the wet/warm season and flexible supports in the dry/cool season in locomotion and postures. There were significant seasonal differences in use of support flexibility in overall positional behavior, and postures (Table 8.7-8; Figure 8.5).

Table 8.7. Seasonal changes in support use of *R. avunculus* in Khau Ca Forest

	Locomotion				Postures				Overall			
	Dry/cool		Wet/warm		Dry/cool		Wet/warm		Dry/cool		Wet/warm	
	n	%	n	%	n	%	n	%	n	%	n	%
Support number:												
Single	566	76.18%	725	76.80%	763	87.50%	927	88.12%	1,329	82.29%	1,652	82.77%
Combined	152	20.46%	158	16.74%	87	9.98%	85	8.08%	239	14.80%	243	12.17%
Multi	20	2.69%	39	4.13%	12	1.38%	14	1.33%	32	1.98%	53	2.66%
Network	5	0.67%	22	2.33%	10	1.15%	26	2.47%	15	0.93%	48	2.40%
Total	*743*	*100.00%*	*944*	*100.00%*	*872*	*100.00%*	*1,052*	*100.00%*	*1,615*	*100.00%*	*1,996*	*100.00%*
Support size:												
Trunk	8	1.08%	22	2.33%	4	0.46%	17	1.62%	12	0.74%	39	1.95%
Bough	129	17.36%	172	18.22%	167	19.15%	223	21.20%	296	18.33%	395	19.79%
Branch	545	73.35%	670	70.97%	630	72.25%	739	70.25%	1,175	72.76%	1,409	70.59%
Twig	41	5.52%	72	7.63%	44	5.05%	68	6.46%	85	5.26%	140	7.01%
Liana	20	2.69%	8	0.85%	27	3.10%	5	0.48%	47	2.91%	13	0.65%
Total	*743*	*100.00%*	*944*	*100.00%*	*872*	*100.00%*	*1,052*	*100.00%*	*1,615*	*100.00%*	*1,996*	*100.00%*
Support orientation:												
Horizontal	348	46.84%	391	41.42%	508	58.26%	518	49.24%	856	53.00%	909	45.54%
Oblique	283	38.09%	360	38.14%	294	33.72%	379	36.03%	577	35.73%	739	37.02%
Vertical	80	10.77%	119	12.61%	21	2.41%	35	3.33%	101	6.25%	154	7.72%
Terminal	29	3.90%	49	5.19%	22	2.52%	37	3.52%	51	3.16%	86	4.31%
Fork	3	0.40%	25	2.65%	27	3.10%	83	7.89%	30	1.86%	108	5.41%
Total	*743*	*100.00%*	*944*	*100.00%*	*872*	*100.00%*	*1,052*	*100.00%*	*1,615*	*100.00%*	*1,996*	*100.00%*
Support flexibility:												
Flexible	372	50.07%	455	48.20%	368	42.20%	375	35.65%	740	45.82%	830	41.58%
Stable	371	49.93%	489	51.80%	504	57.80%	677	64.35%	875	54.18%	1,166	58.42%
Total	*743*	*100.00%*	*944*	*100.00%*	*872*	*100.00%*	*1,052*	*100.00%*	*1,615*	*100.00%*	*1,996*	*100.00%*

Table 8.8. G-tests of seasonal differences in support use by *R. avunculus* in Khau Ca Forest

	Locomotion	**Postures**	**Overall**
Support number:	**13.527 ****	**6.619, n.s.**	**18.246 *****
Single	0.012, n.s.	0.011, n.s.	0.013, n.s.
Combined	2.626, n.s.	1.753, n.s.	4.040, n.s.
Multi	2.440, n.s.	0.007, n.s.	1.706, n.s.
Network	7.758 *	4.598, n.s.	11.703**
Support size:	**15.763 ****	**30.361 *****	**44.268 *****
Trunk	3.807, n.s.	6.344, n.s.	9.773**
Bough	0.146, n.s.	0.822, n.s.	0.839, n.s.
Branch	0.189, n.s.	0.157, n.s.	0.340, n.s.
Twig	2.634, n.s.	1.573, n.s.	4.193, n.s.
Liana	8.448 *	20.712 ***	27.884***
Support orientation:	**20.368 *****	**31.280 *****	**48.247 *****
Horizontal	1.927, n.s.	4.716, n.s.	6.792 *
Oblique	0.0002, n.s.	0.541, n.s.	0.302, n.s.
Vertical	1.075, n.s.	1.363, n.s.	2.547, n.s.
Terminal	1.447, n.s.	1.514, n.s.	3.048, n.s.
Fork	14.675***	19.31 ***	30.736 ***
Support flexibility:	**0.581, n.s.**	**8.635 ****	**6.519 ***
Flexible	0.198, n.s.	3.808, n.s.	2.559, n.s.
Stable	0.189, n.s.	2.079, n.s.	1.819, n.s.

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

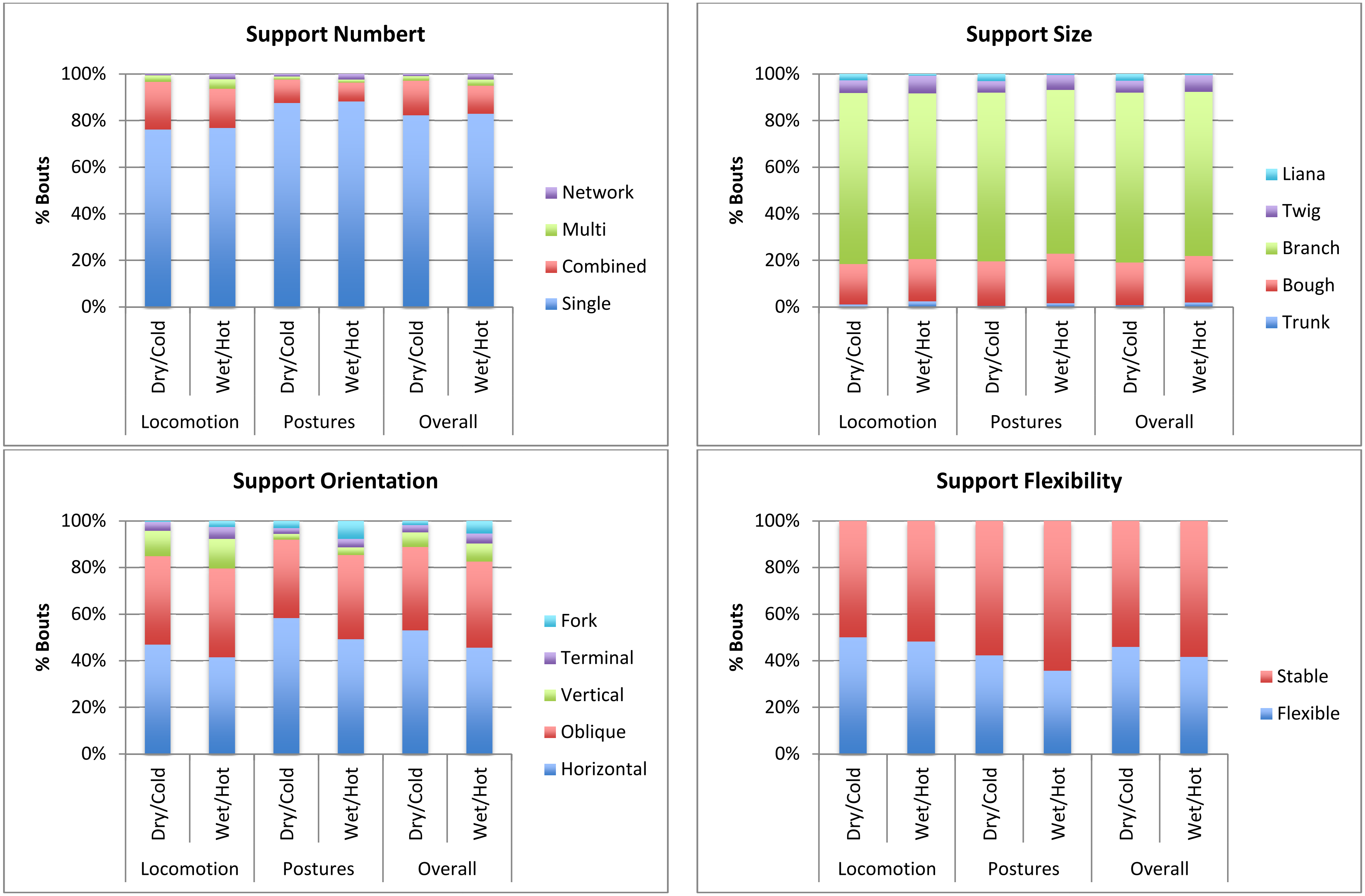

Figure 8.5. Frequencies of support use by seasonal changes in *R. avunculus* in Khau Ca Forest

8.4. Discussion

As outlined above the data supports the hypothesis that *R. avunculus* exhibits significant differences in positional behavior and support use between dry/cool and wet/warm seasons. Significant seasonal differences were seen in maintenance activities, locomotion and postures. Table 8.9 summarizes the major seasonal differences in positional behavior and support use by *R. avunculus* in Khau Ca Forest between the dry/cool and wet/warm seasons in 2009 and 2010.

Table 8.9. Summary of the major seasonal differences in positional behavior and support use by *R. avunculus* in Khau Ca Forest between the dry/cool and wet/warm seasons in 2009 and 2010.

	Dry/cool season	**Wet/warm season**	**Significance**
Maintenance Activity		More travel	n.s.
		More resting	n.s.
	More foraging		**
	More feeding		***
Locomotion	More quadrupedalism		n.s.
	More dropping		*
		More leaping	n.s.
		More climbing	n.s.
		More arm-swinging	n.s.
Postures	More sitting		n.s.
		More standing	n.s.
		More lying	n.s.
		More other postures	***
Support number	More combined supports		n.s.
		More multi supports	n.s.
		More network support	**
Support size	More branches		n.s.
	More lianas		***
		More trunks	**
		More boughs	n.s.
		More twigs	n.s.
Support orientation	More horizontal supports		*
		More oblique supports	n.s.
		More forks	***
Support flexibility	More flexible supports		n.s.
		More stable supports	n.s.

Note. n.s.: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

R. avunculus traveled, rested and displayed more often in the wet/warm season. *R. avunculus* more frequently leaped, climbed and arm-swung in the wet/warm season. Quadrupedalism and drop were occurred more frequently during both travel and foraging in the dry/cool season.

Crompton (1984) found that during the summer period of high temperatures and heavy rainfall, both *Galago senegalensis* and *G. crassicaudatus* climbed significantly more, using the peripheries of tree crowns more, thus using more oblique and small supports that were associated with galago's diets changing from gummivory to insectivory in the summer. Gebo and Chapman (1995a) found that red colobus monkeys (*Colobus badius*) in Kibale Forest, Uganda used slightly more climbing during travel in the wet season than in the dry season. Youlatos (1998b) also found that red howling monkeys (*Alouatta seniculus*) in French Guiana had higher frequencies of clamber (i.e., climbing in this study) in the wet season and this was considered to probably be associated with diet. Thus, the increase in climbing by *R. avunculus* in the wet/warm season is also likely associated with diet. *R. avunculus* increased consumption of fruits and seeds in the wet/warm season, the peak season of fruiting and seeding in Khau Ca Forest [see Chapter 4 of Dong Thanh Hai (2011)]. Contrary to findings of Dagosto (1995), and Youlatos (1998b), but similar to finding of Gebo and Chapman (1995a), *R. avunculus* increased the frequency of leaping in the wet/warm season. There is no clear understanding of why leaping showed seasonal changes (Dagosto, 1995; Gebo and Chapman, 1995a; Youlatos, 1998b).

R. avunculus used quadupedalism less frequently in the wet/warm season. This pattern was similar to that of galagos (Crompton, 1984), red colobus monkeys (Gebo and Chapman, 1995a) and red howling monkeys (Youlatos, 1998b), but opposite of that of lemurs (Dagosto, 1995). There is no clear suggestion of what factor(s) affect seasonal changes in quadrupedalism by primates.

Sit occurred more frequently during resting and feeding in the dry/cool season and this might be related to the low temperatures during this season. Similar to other colobines, *R. avunculus* the high frequency of sitting in the cold might be an energy-saving posture (Dasilva, 1993; Grueter *et al.*, 2013). In contrast, red howling monkeys living in the equatorial climate of French Guiana, sit more frequently in the wet season, and Youlatos (1998b) argued that this might relate to the need to sit on larger supports while processing fruits by special manipulation.

Significant differences in support use of *R. avunculus* between dry/cool and wet/warm seasons might be explained by both their activities and diet. In the dry/cool season, *R. avunculus* foraged and fed more frequently on combined supports of flexible branches and lianas in horizontal orientation, and rested by sitting more frequently on horizontal supports. In the wet/warm season, to acquire fruits and seeds, *R. avunculus* leaped, climbed and arm-swung more frequently on trunks, oblique boughs and twigs, and its postures included more standing, lying and other postures more frequently on stable supports.

In conclusion, previous studies of other primates showed that association between seasonal changes and positional behavior and support use of primates might relate to the shift of diet and foraging/feeding patterns by seasons (Crompton, 1984; Dagosto, 1995; Gebo and Chapman, 1995a; Youlatos, 1998b). In this study, data indicated that *R. avunculus* exhibited seasonal variation in positional behavior and support use in Khau Ca Forest. The seasonal changes in positional behavior and support use of *R. avunculus* is not only associated with diet and foraging/feeding behavior but also by ambient temperatures across the seasons.

Summary

- In Khau Ca Forest, *R. avunculus* significantly differed in maintenance activities between dry/cool and wet/warm seasons. Foraging and feeding significantly increased in the dry/cool season. Travel, resting and displaying were slightly increased in the wet/warm season.
- There were significantly seasonal differences in locomotion. Leaping, climbing, arm-swinging and other locomotion were used more frequently than in the wet/warm season. Quadrupedalism and dropping were used more frequently in dry/cool season.

- Postures were significantly different between the dry/cool and wet/warm seasons. *R. avunculus* used sitting more frequently in the dry/cool season, and used standing, lying, clinging and other postures more frequently in the wet/warm season.
- In the dry/cool season, *R. avunculus* more frequently used combined, flexible branches and lianas in horizontal orientation. Multi and network supports of trunks, boughs and twigs in oblique or forked orientation were used more frequently in the wet/warm season.
- Seasonal changes in positional behavior and support use of *R. avunculus* might be associated with the shift of diet, foraging/feeding behavior, and ambient temperatures by seasons.

CHAPTER IX

SUMMARY AND FINAL DISCUSSION

9.1. Introduction

I described the habitat structure of the Khau Ca Forest, home to more than 100 *R. avunculus*. Secondly, I documented the positional repertoire and support use of adult male *R. avunculus* as a representative baseline for this species. Thirdly, I examined sex- and age-based differences in locomotor and postural patterns of *R. avunculus*. Finally, I tested the influences of seasonal changes on positional behavior and support use for this species in Khau Ca Forest. This chapter summarizes the findings of this study, and discusses the effects of key factors that influence positional behavior and support use of *R. avunculus* in Khau Ca Forest. Study implications and suggestions for future research end this chapter.

9.2. Summary of Findings

The Khau Ca Forest of Ha Giang Province, Vietnam is an ideal location for research and conservation of the critically endangered Tonkin snub-nosed monkeys (Baillie and Butcher, 2012; Covert *et al.*, 2008). This study provides the first quantitative analysis of positional behavior and support use of *R. avunculus* and contributes to an enhanced understanding of behavioral ecology of this understudied species, but the genus *Rhinopithecus* as well. Comparisons with other primates also expand our knowledge on the positional behavior and ecology of primates, particularly for colobines.

The data presented in Chapter IV show that the physical structure of Khau Ca Forest is characterized by tree density of 513 stems/ha, mean tree height of 14 ± 6.8 m, mean DBH of 27.7

± 23.0 cm, total basal area of 45.60 m^2/ha, and mortality rate of 13 stems/ha/year. There were at least 471 vascular plant species belonging to 268 genera, 113 families and 4 phyla recorded in Khau Ca (Nguyen Anh Duc *et al.*, 2006a; 2006b; Vu Anh Tai *et al.*, 2009). *Olea* sp. (Oleaceae), *Polyalthia cerasoides* (Annonaceae), and *Excentrodendron hsienmu* (Tiliaceae) are the most dominant species in the Khau Ca Forest. Plant production (flowering, fruiting, and leafing) patterns differed across the six phenological transects in this study. In the Khau Ca Forest, productivity of fruit was significantly correlated to both temperature and rainfall, and productivity of young leaves was significantly correlated to temperature. The habitat structure at Khau Ca is relatively similar to the habitat structure of forests occupied by other odd-nosed monkeys in Vietnam, Lao PDR, Cambodia and China (Blanc *et al.*, 2000; Dong Thanh Hai, 2011; Grueter, 2009; Ha Thang Long, 2009; Hoang Minh Duc, 2007; Phiapalath, 2009; Rawson, 2009; Ulibarri, 2013). At present, food resources in Khau Ca are estimated to be sufficient to maintain a large *R. avunculus* population.

The positional repertoire of adult male *R. avunculus* is presented in Chapter V. Its locomotor repertoire included nine locomotor modes (19 submodes) and is dominated by quadrupedalism (53.31%), followed by leap (15.56%), climb (13.24%), drop (10.57%), arm-swing (5.23%) and other locomotor behaviors (2.09%). There were no significant differences in positional behaviors during travel and foraging; leap, climb and drop were used much more frequently during travel than during foraging, and arm-swing was used only during travel. Postural repertoire included six postural modes (16 submodes) and is dominated by sitting (81.13%), and followed by stand (13.42%), lie (2.1%), cling (1.78%) and other postures (1.57%). There was significant independence in postures and associated maintenance activities. Sit and stand were the most common postures overall, whereas lie was most frequent in social behaviors and periods of rest. Cling was the most frequently observed in displaying. During associated maintenance activities, *R. avunculus* most frequently used single and combined supports of branches and boughs on horizontal and oblique orientation. Flexible supports were most often used during foraging and feeding while stable supports were preferred during travel, resting and other activities. In comparison to other colobines, the positional behavior data of adult male *R. avunculus* provides additional evidence of a complex relationship between body size effects and positional behavior and support use by African and Asian colobines.

The sex-based differences between adult males and females presented in Chapter VI indicated that smaller-bodied adult females more frequently foraged, fed and participated in social behaviors than larger-bodied adult males. There were no significant differences between adult males and females during travel and foraging. The locomotion of both males and females was dominated by quadrupedalism, followed by leap, drop, arm-swing and other locomotion. In postures, there were only significant differences between adult males and females in overall postural behaviors, during resting, and during social behaviors. Adult males and females differed significantly in stand during resting, and lie during social behavior. Regarding support use, adult males and females did not differ significantly in use of support number, size, and orientation. There were significant differences between adult males and females in use of support flexibility. In locomotion, adult females used stable supports more frequently than did males during travel. In postures, adult females used stable supports more frequent than males during resting, feeding and displaying. This study indicated that sex-related differences in body size influenced the positional behavior and support use of adult male and female *R. avunculus*, but these differences were not consistent with predictions based on the work of Cartmill and Milton (1977), and Fleagle and Mittermeier (1980).

In Chapter VII, the data showed that there were significant age-based differences in positional behavior and support use of *R. avunculus.* In locomotion, larger-bodied adults climbed more frequently, and leaped less frequently than smaller-bodied juveniles and infants during travel. In posture, the frequency of sitting increase with increasing ages during resting and feeding. In locomotion and posture, adults tended to use larger support and flexible supports more frequently than juveniles and infants. Thus, this analysis illustrated age-based differences in body size influenced the positional behavior and support use of *R. avunculus*, but again these differences are not consistent with predictions based on the work of Fleagle and Mittermeier (1980).

The analysis presented in Chapter VIII demonstrates that maintenance activities, positional behavior and support use of *R. avunculus* were significantly different between dry/cool and wet/warm seasons. In the dry/cool season, *R. avunculus* foraging and feeding was significantly more frequent than in the wet/warm season. Quadrupedalism, dropping, and sitting were also more frequent in the dry/cool season as was the use of combined supports of flexible branches and lianas in horizontal orientation. In the wet/warm season, *R. avunculus* slightly increased the frequencies of travel, rest and display. For locomotion, leaping, climbing, arm-swinging and other locomotion were used more frequently. For posture, standing, lying, clinging and other postures were used more frequently. Multiple and network supports of trunks, boughs and twigs in oblique or forked orientation were used more frequently in the wet/warm season. Seasonal changes in positional behavior and support use of *R. avunculus* might be associated with shifts of diet, foraging/feeding behavior, and ambient temperatures by season.

9.3. What are the Relationships between Positional Behavior and Support Use of *R. avunculus*?

As mentioned above, this study provides the first quantitative data on positional behavior and support use of *R. avunculus*. The analyses also indicate complexity in positional behavior and support use of *R. avunculus*. According to Garber (2011), positional behavior and support use of a species are influenced by a set of physiological, ecological, and social and behavioral factors. Recent studies have provided several possible explanations for intra- and interspecific differences in primate positional behavior including anatomy, diet, substrate availability and habitat differences (e.g., Bitty and McGraw, 2007; Cant, 1992; Covert *et al.*, 2004; Dagosto and Yamashita, 1998; Doran, 1992b, 1993; Fleagle, 1976b, 1977; Fleagle and Mittermeier, 1980; Garber and Pruetz, 1995; Gebo, 1992; Gebo and Chapman, 1995a; McGraw, 1996a, 1996b, 2000; Workman and Schmitt, 2012).

Body size and limb proportion have received the most attention in studies of primate positional behavior (e.g., Cant, 1992; Doran, 1993; Fleagle, 1976a, 1976b; Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995b; Johnson and Shapiro, 1998; Jungers, 1984; Lawler, 2006). The ratio of forelimb length to hindlimb length, the intermembral index (IMI), seems to correlate with locomotor patterns of primates (Fleagle, 2013; Jungers, 1985). It should also be remembered, as noted by Fleagle (2013), some phylogenetic controls are important to fully understand the relationships between body proportions and locomotion. According to Fleagle (2013) and Jungers (1985), arboreal and terrestrial quadrupeds have forelimbs and hindlimbs that are relatively similar in length (70 < IMI ≤ 100); leapers have longer hind limbs and shorter, slender forelimbs (IMI < 70); suspensory primates having forelimbs are longer than hindlimbs (IMI > 100); bipeds have stronger, longer legs and slender, shorter arms. Because there is not a single skeleton of an adult *R. avunculus* in any museum collection, we do not know the IMI for *R. avunculus*. Based on visual comparisons of *R. avunculus* with other odd-nosed monkeys, it appears to have a more slender body and longer tail longer than the more semi-terrestrial snub-nosed monkeys, and more closely resemble the arboreal doucs (see Table 2.2). From field observation and photographs, I presume *R. avunculus* has IMI ≈ 100 (Figure 9.1). Relative limb lengths (i.e., IMI) are still considered to have a meaningful relationship with a locomotor tendency for living and fossil primates. However, the analyses of Workman and Covert (2005), Workman and Schmitt (2012), and Xiong *et al.* (2009) did not demonstrate a strong relationship between IMI and locomotor behaviors, in particular frequency of leaping in Old World monkeys.

Figure 9.1. An adult male *R. avunculus* in lateral view showing relative comparison between its forelimbs and hindlimbs in length

Body size is central to most studies of primate positional behavior, and there is a significant amount of research that has demonstrated a strong relationship between body size and positional behavior among primates (e.g., Bitty and McGraw, 2007; Dagosto, 1994; Doran, 1992b, 1993; Fleagle and Mittermeier, 1980; Garber, 1991; Gebo and Chapman, 1995b; McGraw, 1998a, 1998b, 2000; Youlatos, 1998a). As noted earlier Fleagle and Mittermeier (1980, p. 309) suggested “leaping to decrease with an increase in body size and climbing to increase with size”, where Cartmill and Milton (1977, p. 269) argued that “the important of suspensory locomotion and postures in an arboreal animal’s repertoire …as a function of its body weight, since a large animal must find it easier to hang below a relatively small branch than to balance atop it”. In terms of support use, larger-bodied animals tend to use larger supports or greater number of supports than would smaller-bodied animals (Fleagle and Mittermeier, 1980). Finally, larger-bodied primates having relative longer forelimbs likely find it easier to grasp and climb on large vertical supports or highly inclined supports (Cant, 1992; Jungers, 1985). My data showed the association between body size and positional behavior in *R. avunculus* fit theoretical predictions for a large-bodied arboreal primate that leaping (McGraw, 1998a), climbing and arm-swinging were important in the locomotor repertoire of *R. avunculus*. *R. avunculus* preferred stable branches and boughs in horizontal and oblique orientation. However, the association between body size and positional behavior are not consistent for all living primates; and there is a dramatic adult body mass range of less than 50 g (the smallest mouse lemurs) to about 180 kg (adult male lowland gorillas) (Fleagle, 2013; Jungers, 1985). For example, Crompton (1984) studied two galago species and his results supported predictions based on body size by Fleagle and Mittermeier (1980). Gebo and Chapman (1995b) found no clear intra- and interspecific differences in locomotor behavior and substrate use by five species of *Cercopithecus* and *Colobus* in Kibale Forest. In contrast, McGraw (1998a, 1998b) found a different association between body size and locomotion between colobines and cercopithecines in Tai Forest where the smallest colobines leaped the most, and the largest cercopithecines leaped the most. My data also indicated that sex- and age-based differences in body size influenced positional behavior and support use of *R. avunculus,* but these differences did not consistently follow predictions based on body size. Together with available data on other colobines, the positional behavior data of *R. avunculus* provides evidence of a complex relationship between body size, positional behavior, and support use by African and Asian colobines.

The relative abundance and distribution of food resources affect the time and the pattern of locomotion invested in searching for these resources. The distribution of food sources also affects positional behavior and support use in arboreal primates. In Khau Ca, *R. avunculus* consumes a variety of food types; leaf stems and fruits are the most common part of the their diet, followed by young leaves, unripe fruit, inflorescences and flowers, and seeds (Covert *et al.*, 2008; Dong Thanh Hai, 2011; Le Khac Quyet *et al.*, 2007). These food types are abundant in Khau Ca Forest and this species does not need to invest a great deal of time for foraging and feeding similar to many other colobines; however, these food types are mainly distributed on small, flexible twigs or lianas. *R. avunculus* used more climbing during foraging, and used more terminal supports (twigs) while both foraging and feeding than cercopithecines. This result is similar to positional behavior and support use of cercopithecids in the Tai Forest (McGraw, 1998a, 1998b). In contrast, Chinese snub-nosed monkeys live in challenging, high mountane habitats where food resources are scarce in the winter. They adapt to this by being semi-terrestrial animals spending a large amount of time foraging and feeding on the ground (Bleisch *et al.*, 1993; Bleisch and Xie, 1998; Grueter *et al.*, 2013; Isler and Gruter, 2006; Su *et al.*, 1998). Similar to other leaf-eating monkeys, high frequency of sitting by *R. avunculus* might be an energy-saving strategy needed to more effectively digest their high fiber diets (Kay and Davies, 1994).

Studies of Dagosto (1995), Gebo and Chapman (1995a), Lemelin and Schmitt (2004), and Youlatos (1998b) found that positional behavior during feeding may be associated with seasonal changes in diet, foraging strategies, and availability and distribution of feeding sites. My data demonstrated that there were significant differences in positional behavior and support use by *R. avunculus* between the dry/cool and wet/warm seasons in Khau Ca Forest. Seasonal changes in fruit and leaf production of Khau Ca Forest likely influence the frequency of climbing, and substrate preference of *R. avunculus*. Seasonal changes in ambient temperature likely influence the frequency of sitting which in turn might reflect an energy-saving strategy (Dasilva, 1993; Grueter *et al.*, 2013).

Habitat structure has been documented to influence positional behavior and support use of primates (Dagosto, 1995; Dagosto and Yamashita, 1998; Garber, 1984; Garber and Pruetz, 1995; McGraw, 1998a, 1998b; Remis, 1995). As recent data on population distribution suggests that *R. avunculus* depends on the near pristine forest areas, Khau Ca Forest has the best quality and safe habitat for *R. avunculus*, as the habitats in Na Hang and Cham Chu Nature Reserves (Tuyen Quang Province), and Tung Vai Forest (Ha Giang Province) are highly disturbed and degraded due to human activities (e.g., agricultural encroachment, timber extraction, and hunting). It is possible that there are some understudied characteristics in the structure of the Khau Ca Forest that influence positional behavior and support use of *R. avunculus* such as gaps in the canopy, food distribution, and food tree architecture. In addition, the relative lack of hunting in the Khau Ca Forest compared to the other sites may be a nearly equally important factor for the health of this *R. avunculus* population.

9.4. Recommendations for Future Studies

Although this study was only carried out at one site in the Khau Ca Forest, the results have provided data on positional repertoire and relationships among positional behavior and support use, body size, ontogeny, and seasonal changes for *R. avunculus*. The results can be used to generate predictions for future research on positional behavior and support use of *R. avunculus* and other odd-nosed monkeys as well. However, there are many questions relevant to the positional behavior of *R. avunculus* that should be addressed in future research such as that identified in the following recommendations.

I further recommend that future work adhere to the methods set out in this dissertation for collecting more data on positional behavior and support use of *R. avunculus* in Khau Ca and other locations in Na Hang Nature Reserve and Tung Vai Forest. It is important for intraspecific comparison between different sites to evaluate habitat and support preferences, and the impact of forest disturbance and fragmentation on positional behavior patterns of *R. avunculus*.

I acknowledge that this study lacks data on height and canopy use, and gap crossing behavior of *R. avunculus*. I would recommend future research to collect these data for a deeper understating of positional behavior and habitat use of *R. avunculus*. Further studies in behavior and ecology, such as social behavior and organization, feeding ecology, and home range and ranging behavior also are needed to improve our knowledge on this species. From videography-based data collection, data should be collected for studies of tail use, gait choice and kinematic analysis, which will shed light on the biomechanics in positional behavior of *R. avunculus.*

9.5. Broader Implications

Overall, my dissertation has shown that sex- and age-based difference in body size, and seasonal changes influence positional behavior and support use of *R. avunculus*. This study has provided a background of *R. avunculus*' positional behavior from which other hypotheses regarding the positional behavior of other living odd-nosed monkeys in particular and Asian colobines in general, can be generated. Moreover, data on positional behavior and habitat use of

R. avunculus and other odd-nosed monkeys would be important to reconstruct locomotor behavioral ecology of fossil odd-nosed monkeys including *Mesopithecus*.

My study has also suggested that patterns of postional behavior and support use might be an energy-saving strategy of *R. avunculus* to adapt to dietary constraints and environmental temperatures. It is important for understanding subtle variation in the positional behavior of a species in its ecological context, and might be beneficial for our interpretations of the fossil record regardless of existing form function associations.

At present, non-human primates include some most endangered mammalian species in the world. Main threats to primates include hunting and poaching activities, habitat loss and degradation, and illegal trade (Chapman and Peres, 2001; Cowlishaw and Dunbar, 2000). Chapman and Peres (2001), and Marsh *et al.* (2003) argued that future efforts to conserve forest fragments that are increasingly critical to endangered primate communities require generating a spirit of cooperation with local communities, providing alternatives and incentives to locals to resist deforestation, and an ability by researchers to consider conservation within the context of the economic, political, and social needs of surrounding human populations, not just from the perspective of the primates. As Marsh *et al.* (2003) noted, much more research is needed to fully understand the affects or implications of conservation initiatives and to develop a broader understanding of how to manage forest fragmentation while protecting the health, behavioral and morphological diversity, and self-sufficiency of the primates that live there. In conjunction with the dedication and the on-going work of researchers and conservationists, I hope that this study contributes to a greater understanding of the plasticity of behavioral ecology generally, and more specifically the positional behavior and support use of *R. avunculus* in Khau Ca Forest.

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APPENDICES

Appendix 1. Video hours of positional behavior of *R. avunculus* collected from January 2009 to December 2010

	2009		**2010**	
	Number of Days	Observational Hours	Number of Days	Observational Hours
JAN	5	9	9	27
FEB	5	7	5	18
MAR	5	12	6	21
APR	3	10	4	8
MAY	7	18	8	15
JUN	4	10	9	31
JUL	5	10	9	19
AUG	9	26	4	12
SEP	5	14	3	6
OCT	4	11	7	16
NOV	11	33	9	19
DEC	7	26	5	7
Total	*70*	*186*	*78*	*199*

Appendix 2. List of plant species recorded on six transects and 30 plots in Khau Ca Forest

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
I.	**Aceraceae**	**24**	**57**	**81**
1.	*Acer brevipes*	10	20	30
2.	*Acer fabri*	1	8	9
3.	*Acer tonkinense*	13	27	40
4.	*Acer* sp.		2	2
II.	**Actinidiaceae**	**3**	**2**	**5**
5.	*Saurauia fasciculata*	3	2	5
III.	**Alangiaceae**		**1**	**1**
6.	*Alangium chinense*		1	1
IV.	**Anacardiaceae**	**33**	**30**	**63**
7.	*Mangifera minutifolia*		2	2
8.	*Mangifera* sp.		1	1
9.	*Semecarpus* sp.	33	27	60
V.	**Annonaceae**	**188**	**185**	**373**
10.	*Alphonsea* sp.	1		1
11.	*Enicosanthelum* sp.	7	2	9
12.	*Melodorum vietnamense*	5		5
13.	*Miliusa sinensis*	30	15	45
14.	*Miliusa* sp.	1		1
15.	*Polyalthia cerasoides*	64	117	181
16.	*Polyalthia suberosa*		2	2
17.	*Polyalthia thorelii*	59	38	97
18.	*Polyalthia* sp.	21	11	32
VI.	**Apocynaceae**	**2**	**3**	**5**
19.	*Tabernaemontana bovina*	2	1	3
20.	*Wrightia pubescens*		2	2
VII.	**Aquifoliaceae**	**11**	**23**	**34**
21.	*Ilex crenata*		1	1
22.	*Ilex* sp.	11	22	33
VIII.	**Araliaceae**	**5**	**14**	**19**
23.	*Schefflera pes-avis*		5	5
24.	*Schefflera* sp.	2	6	8
25.	*Trevesia palmata*	3	3	6
IX.	**Arecaceae**	**2**	**1**	**3**
26.	*Caryota urens*	2		2
27.	*Sabrinus cochinchinensis*		1	1
X.	**Bignoniaceae**	**5**	**10**	**15**
28.	*Radermachera ignea*	5		5
29.	*Radermachera sinica*		10	10

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
XI.	**Burseraceae**	**19**	**25**	**44**
30.	*Canarium album*	3	7	10
31.	*Canarium tramdenum*	13	14	27
32.	*Garuga pinnata*	3	4	7
XII.	**Buxaceae**		**2**	**2**
33.	*Buxus* sp.		2	2
XII.	**Caprifoliaceae**		**1**	**1**
34.	*Viburnum* sp.		1	1
XIII.	**Celastraceae**	**6**	**46**	**52**
35.	*Celastrus* sp.	6	46	52
XIV.	**Clusiaceae**	**83**	**87**	**170**
36.	*Calophyllum* sp.		10	10
37.	*Cratoxylum formosum*	8	3	11
38.	*Garcinia bracteata*	54	36	90
39.	*Garcinia fagraeoides*	4	22	26
40.	*Garcinia paucinervis*	16	15	31
41.	*Garcinia* sp.	1	1	2
XV.	**Dilleniaceae**	**1**		**1**
42.	Dillenia hookeri	1		1
XVI.	**Ebenaceae**	**42**	**19**	**61**
43.	*Diospyros montana*	3	5	8
44.	*Diospyros nitida*		10	10
45.	*Diospyros* sp.	39	4	43
XVII.	**Elaeocarpaceae**	**24**	**24**	**48**
46.	*Elaeocarpus griffithii*		11	11
47.	*Elaeocarpus* sp.	3	1	4
48.	*Sloanea sinensis*	21	12	33
XVIII.	**Ericaceae**	**1**	**2**	**3**
49.	*Rhododendron* sp.	1	2	3
XIX.	**Euphorbiaceae**	**73**	**117**	**190**
50.	*Antidesma bunius*	4	7	11
51.	*Antidesma montanum*	19		19
52.	*Antidesma* sp.	7	33	40
53.	*Bridelia balansae*	1	2	3
54.	*Croton* sp.	14		14
55.	*Deutrianthus tonkinensis*	2		2
56.	*Macaranga* sp.	6		6
57.	*Mallotus barbatus*		1	1
58.	*Triadica rotundifolia*	2		2
59.	*Triadica sebiferum*		6	6
60.	*Trigonostemon* sp.	16		16

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
61.	*Vernicia fordii*		1	1
62.	*Vernicia montana*	2	67	69
XX.	**Fabaceae**	**9**	**2**	**11**
63.	*Archidendron balansae*	1		1
64.	*Archidendron poilanei*	7	2	9
65.	*Peltophorum dasyrrachis*	1		1
XXI.	**Fagaceae**	**31**	**102**	**133**
66.	*Castanopsis* sp.	15	50	65
67.	*Fagus* sp.		1	1
68.	*Lithocarpus bentramensis*		4	4
69.	*Lithocarpus* sp.	16	22	38
70.	*Quercus* sp.		25	25
XXII.	**Flacourtiaceae**	**8**	**9**	**17**
71.	*Gonocaryum lobbianum*		**3**	**3**
72.	*Hydnocarpus kurzii*	6	3	9
73.	*Hydnocarpus* sp.	2	3	5
XXIII.	**Hammamelidaceae**		**1**	**1**
74.	*Altingia poilanei*		1	1
XXIV.	**Icacinaceae**		**5**	**5**
75.	*Gomphandra tetrandra*		5	5
XXV.	**Illiciaceae**		**14**	**14**
76.	*Illicium parvifolium*		13	13
77.	*Illicium tenuifolium*		1	1
XXVI.	**Iteaceae**	**1**	**1**	**2**
78.	*Itea chinensis*	1		1
79.	*Itea* sp.		1	1
XXVII.	**Juglandaceae**	**5**	**38**	**43**
80.	*Carya tonkinensis*	2		2
81.	*Platycarya strobilacea*	1	38	39
82.	*Pterocarya tonkinensis*	2		2
XXVIII.	**Lamiaceae**	**18**	**41**	**59**
83.	*Gmelina* sp.	18	41	59
XXIX	**Lauraceae**	**133**	**147**	**280**
84.	*Beilschmiedia* sp.	3	9	12
85.	*Caryodaphnopsis tonkinensis*	7	1	8
86.	*Caryodapnopsis* sp.	1		1
87.	*Cinnamomum iners*		1	1
88.	*Cinnamomum* sp.	3	3	6
89.	*Lindera* sp.		33	33
90.	*Litsea brevipes*		11	11
91.	*Litsea cubeba*		1	1

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
92.	*Litsea* sp.		6	6
93.	*Machilus platycarpa*	44	15	59
94.	*Machilus* sp.	2	10	12
95.	*Neocinnamomum* sp.		1	1
96.	*Neolitsea buisanensis*	1		1
97.	*Neolitsea* sp.	7		7
98.	*Phoebe kunstleri*	25	53	78
99.	*Phoebe* sp.	40	3	43
XXX.	**Linaceae**	**1**	**4**	**5**
100.	Tirpitzia sinensis	1	4	5
XXXI.	**Magnoliaceae**		**8**	**8**
101.	*Magnolia* sp.		1	1
102.	*Michelia foveolata*		5	5
103.	*Michelia* sp.		2	2
XXXII.	**Malvaceae**	**4**		**4**
104.	*Hainania trichosperma*	2		2
105.	*Hainania* sp.	2		2
XXXIII.	**Meliaceae**	**52**	**49**	**101**
106.	*Aglaia* sp.	33	35	68
107.	*Aphanamixis grandifora*	1		1
108.	*Aphanamixis* sp.		11	11
109.	*Chisocheton* sp.	7	1	8
110.	*Dysoxylum* sp.	8	2	10
111.	*Walsura robusta*	3		3
XXXIV.	**Mimosaceae**	**1**		**1**
112.	*Pithecellobium* sp.	1		1
XXXV.	**Moraceae**	**3**	**8**	**11**
113.	*Ficus henryi*		1	1
114.	*Ficus virens*	1	6	7
115.	*Ficus* sp.	2	1	3
XXXVI.	**Myrsinaceae**	**3**	**9**	**12**
116.	*Ardisia* sp.		1	1
117.	*Myrsina affinis*	3		3
118.	*Myrsina linearis*		3	3
119.	*Myrsina seguinii*		5	5
XXXVII.	**Myrtaceae**	**45**	**35**	**80**
120.	*Cleistocalyx* sp.		1	1
121.	*Decaspermum* sp.		9	9
122.	*Syzygium cuminii*	7	2	9
123.	*Syzygium jambos*	9	3	12
124.	*Syzygium* sp.	29	16	45

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
125.	*Syzygium zeylanicum*		4	4
XXXVIII.	**Oleaceae**	**96**	**118**	**214**
126.	*Linociera pierrei*		11	11
127.	*Olea* sp.	96	107	203
XXXIX.	**Opiliaceae**	**1**	**3**	**4**
128.	*Meliantha suavis*	1	3	4
XL.	**Podocarpaceae**	**7**	**8**	**15**
129.	*Nageia fleuryi*	6	3	9
130.	*Nageia wallichiana*		3	3
131.	*Podocarpus nerrifolius*		2	2
132.	*Podocarpus* sp.	1		1
XLI.	**Proteaceae**	**1**		**1**
133.	*Helicia* sp.	1		1
XLII.	**Rhamnaceae**	**3**	**5**	**8**
134.	*Ziziphus oenoplia*		5	5
135.	*Ziziphus* sp.	3		3
XLIII.	**Rosaceae**		**7**	**7**
136.	*Prunus fordiana*		3	3
137.	*Prunus* sp.		4	4
XLIV.	**Rubiaceae**	**37**	**40**	**77**
138.	*Aidia cochinchinensis*	8	10	18
139.	*Aidia oxyodonta*	16	24	40
140.	*Gardenia* sp.	5	1	6
141.	*Meyna* sp.		3	3
142.	*Mycetia* sp.		1	1
143.	*Nauclea orientalis*	4		4
144.	*Nauclea* sp.	3	1	4
145.	*Randia* sp.	1		1
XLV.	**Rutaceae**	**8**	**13**	**21**
146.	*Clausena harmandiana*		1	1
147.	*Clausena heptaphylla*		2	2
148.	*Clausena indica*	3	4	7
149.	*Clausena* sp.	2		2
150.	*Euodia meliaefolia*	2	4	6
151.	*Glycosmis* sp.		1	1
152.	*Micromelum hirsutum*	1		1
153.	*Skimma* sp.		1	1
XLVI.	**Sabiaceae**	**6**	**13**	**19**
154.	*Meliosma simplicifolia*		1	1
155.	*Meliosma* sp.	6	12	18
XLVII.	**Salicaceae**	**15**	**5**	**20**

No.	Family / *Species*	Plots (n)	Transects (n)	Total (n)
156.	*Casearia membranacea*	14	5	19
157.	*Flacourtia* sp.	1		1
XLVIII.	**Sapindaceae**	**49**	**56**	**105**
158.	*Dimocarpus* sp.		2	2
159.	*Nephelium* sp.	2	1	3
160.	*Paranephelium spirei*	8	3	11
161.	*Pometia pinnata*	3	11	14
162.	*Sapindus saponaria*	25	22	47
163.	*Sapindus* sp.	11	17	28
XLIX.	**Sapotaceae**	**4**	**12**	**16**
164.	*Madhuca pasquieri*	2	2	4
165.	*Sinosideroxylon wightianum*	2	10	12
L.	**Sterculiaceae**		**2**	**2**
166.	*Sterculia nobilis*		2	2
LI.	**Styracaceae**	**10**	**25**	**35**
167.	*Styrax serrulatus*	2	4	6
168.	*Styrax tonkinensis*	8	21	29
LII.	**Symplocaceae**	**5**		**5**
169.	*Symplocos* sp.	5		5
LIII.	**Taxaceae**	**1**	**10**	**11**
170.	*Taxus chinensis*	1	10	11
LIV.	**Tiliaceae**	**37**	**50**	**87**
171.	*Excentrodendron tonkinense*	37	50	87
LV.	**Ulmaceae**	**61**	**44**	**105**
172.	*Celtis japonica*	48	21	69
173.	*Celtis sinensis*		4	4
174.	*Celtis tetrandra*		19	19
175.	*Celtis* sp.	13		13
LVI.	**Urticaceae**	**16**	**22**	**38**
176.	*Debregeasia squamata*		2	2
177.	*Dendrocinde urentissima*	7	13	20
178.	*Pouzolzia* sp.		2	2
179.	*Villebrunea* sp.	9	5	14
LVII.	**Verbenaceae**	**12**	**12**	**24**
180.	*Premna* sp.	9	12	21
181.	*Vitex pentaphylla*	1		1
182.	*Vitex trifolia*	2		2
	Grand Total	*1,205*	*1,567*	*2,772*