The foraging ecology of the Delacour's langur (*Trachypithecus delacouri*) in Van Long Nature Reserve, Vietnam

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
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ABSTRACT

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Abstract

Delacour's langurs (*Trachypithecus delacouri*), one of the six limestone langur taxa of Southeast Asia, inhabit isolated, rugged limestone karst mountains in northern Vietnam. The reason for their current restriction to this habitat is unclear. One explanation is that the rocky karst outcrops provide limestone langurs a refuge in a dramatically anthropogenically-altered landscape. Alternatively, several ecological explanations have been proposed to account for their distribution, even though the ecology of wild Delacour's langurs had yet to be studied. In this dissertation, I quantified the foraging ecology of Delacour's langurs living on Dong Quyen Mountain in Van Long Nature Reserve, Vietnam to address the question of whether these langurs show special adaptations to limestone karst or if they are exploiting a refuge habitat into which they have been pushed. I quantify their foraging ecology by systematically investigating their diet and feeding ecology, the chemisty of their eaten leaves, and the types of locomotions and substrates they utilized.

From August 2007 through July 2008, I used instantaneous focal-animal sampling during all-day follows of Delacour's langurs on Dong Quyen Mountain. I collected data on activity budget, diet, and positional behavior. I also collected samples of soils and eaten and uneaten leaves which were tested for phytochemical content.

With nearly 79% leaves in the diet, 60% of which were young leaves, Delacour's langurs are among the most folivorous of studied colobines, and- along with the closely related *T. poliocephalus leucocephalus* of southern China- the most folivorous of the Asian langurs. None of the plants that were important in the Delacour's langur diet were endemic limestone plants, and therefore feeding dependence alone cannot explain the current distribution of limestone langurs on karst habitat. Langurs ate leaves with high protein:fiber ratios, and despite a high percentage of carbon in the soil, young leaves were available throughout the year and plant defenses did not seem to have a large impact on eaten leaves. Delacour's langurs spent nearly 80% of their time on rocks. Quadrupedalism was their dominant locomotor style, more than double that of climbing. Terrestrialism, however, does not adequately describe the dangerous locomotion of these langurs; they are cliff-climbers. Delacour's langurs leapt only 6% of the time, much less than other African and Asian colobines, but their morphology (intermembral index) does not suggest terrestrialism or an evolutionary adaptation for limestone karst. Delacour's langurs appear to be a flexible taxon occupying a refuge habitat into which they have pushed. However, this restricted limestone habitat does not appear limiting in resources. The population at Van Long Nature Reserve is increasing which means that- if protected- this local population can rebound. Persistent hunting for

traditional medicine and the more recent emergence of quarrying limestone for cement, however, threatens their survival.

Dedication

For my parents, Elizabeth and Claude.

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There were moments that I was awed by what I saw in the field and moments that I wept. Both types of moments shaped me and this work, and I am grateful.

1. Introduction

The Colobinae are diverse, ranging widely in their feeding habits, locomotor patterns, and habitat occupation. In addition to leaves, colobines eat considerable amounts of whole fruit, seeds, lichen, and soil (Gautier-Hion, 1978; McKey, 1978; Davies, 1991; Dasilva, 1992; Davies, 1994; Kay and Davies, 1994; Fashing, 2001a; Yang and Zao, 2001; Chapman et al., 2002a; Ding and Zhao, 2004; Sayers and Norconk, 2008; Grueter, 2009a; Matsuda et al., 2009a). Many colobines are arboreal quadrupeds, while some arm-swing habitually and others scale rocky precipices and sleep nightly in shelters (Ripley, 1979; Gebo and Chapman, 1995a; McGraw, 1996; Workman and Covert, 2005; Zhou et al., 2009b). Colobines inhabit the dry climate of northern India to the high altitude conifer forest mountains of Tibet and China and all types of tropical and subtropical African and Asian forests in between (Jay, 1965; Xiao et al., 2003; Fashing, 2007; Kirkpatrick, 2007; Ren et al., 2008; Sayers and Norconk, 2008; Matsuda et al., 2009b). The reason for past successful speciation and current persistence in fragmented and degraded habitats might be because this primate subfamily consists of generalized herbivores capable of utilizing a wide range of ecological niches.

One of the most exciting examples of colobine diversity is the burgeoning information on the so-called 'limestone langurs' of northern Vietnam, southern China, and eastern Laos. The limestone langurs are a monophyletic group of six alloptaric taxa in the genus *Trachypithecus (T. poliocephalus, T. p. leucocephalus, T. francoisi, T. delacouri, T.*

laotum, T. l. hatinhensis) which are presently distributed almost exclusively on limestone karst habitat (Nadler et al., 2004; Table 1; Figure 1). The occupation of mountainous limestone karst habitat by this clade has broadened our understanding of the range of habitats colobines can occupy and the ecological flexibility they possess, due to the specific characteristics of limestone karst.

Covering 400,000 square kilometers (Clements et al., 2006), karst habitat of Southeast Asia is characterized by sharp, exposed rock and vertical cliffs, by stunted and endemic vegetation, by thin, dry, and alkaline soils, by extremes of cold winters and hot summers, and by the presence of caves and rock shelters (Urich, 1989; Whitmore, 1990; Li et al., 2003; Day and Chenoweth, 2004; Liu et al., 2004Sterling et al., 2006; Zhao et al., 2008). Soil depth greatly influences the vegetation on karsts. Karst habitats with thinner soils and much exposed rock contain many herbaceous species, while karstic areas with deeper soils harbor larger trees (Clements et al., 2006). In Vietnam, Phong Nha-Ke Bang National Park and Khau Ca Forest include many very large trees (personal observation; Bert Covert, personal communication) while Van Long Nature Reserve harbors mostly climbers, herbs, and stunted woody plants (Chapter 4). Further, This unique mélange of karstic traits and the exclusive distribution of limestone langurs on them lead to several hypotheses to explain the relationship between limestone langurs and karst habitat: refuge after the loss of non-karst habitat; the presence of special or endemic foods;

protection from predators by use of sleeping sites; shelter against climatic conditions; and the presence of water.

The area of eastern Indochina and southern China was one of the key rainforest refugia for primates during Pleistocene changes in sea level (Gupta and Chivers, 1999). Though natural history is limited, it might be that limestone karst mountains provided island refuges that these langurs colonized in rare events; gene flow was not maintained to prevent speciation and langurs developed adaptations to the karst habitats (Weitzel, 1992). Weitzel's proposal might explain why the limestone langurs are mostly allopatric outliers among typically sympatric Asian langurs (although *T. p. leucocephalus* and *T. francoisi* may be sympatric in parts of their range in southern China (Smith and Yan Xie, 2008)). Citing present-day allopatry as an explanation for their reproductive isolation and consequent speciation is immune to testing or challenging (Thorpe, 2005) and intense hunting pressure precludes a solely ecological explanation of limestone langur distribution and abundance on karst habitats. A similar ecological conundrum of African primate communities has been addressed by Struhsaker (1999). He notes that the present-day distribution of many species may be the artifact of recent hunting, rather than the result of long-time evolution. Anthropogenic effects of hunting, habitat alteration and fragmentation, and deforestation on primate communities have in fact been so pervasive and severe for the last 50 years that their consideration in any ecological analysis is required (Tutin and White, 1999).

Foraging (feeding and locomotion) is an appropriate lens through which to study adaptation. Several studies have examined relationships between locomotion, diet, and the underlying morphology (Fleagle and Mittermeier, 1980; Gebo, 1992; Gebo and Chapman, 1995b), and recognizing dietary variation facilitates a better understanding of differences in morphology and positional behavior (Chapman et al., 2002a). Further, recognizing dietary flexibility helps us better understand the ability of different species to exploit and thrive in various habitats and therefore is useful in developing conservation management plans (Chapman et al., 2002a).

1.1 Research Questions

Do Delacour's langurs (*Trachypithecus delacouri*) show special adaptations to limestone karst or is it a refuge habitat into which they have been pushed? Being that northern Vietnam is the most deforested part of the country, and that karst is unusable for agriculture, karst might provide the last available habitat islands in a sea of rice fields. Alternatively, there may be aspects of the Delacour's langurs' foraging ecology (diet and locomotion) that indicate an older and exclusive relationship with this habitat. This study will address the following four main research questions and their accompanying hypotheses:

1. What is the Delacour's langurs' feeding ecology and how prominently do endemic limestone plants factor into their diet? For the limestone langur species from which wild feeding data exist (*Trachypithecus poliocephalus leucocephalus, T. francoisi*), they do not seem restricted to limestone endemic plants. At the Endangered Primate Rescue Center in northern Vietnam, *Trachypithecus delacouri, T. laotum, T. laotum hatinhensis*, and *T. poliocephalus* eat the leaves, bark, flowers, and fruit from more than 100 species, but less than 10% of these are typical limestone species (Tilo Nadler, personal communication).

2. What is the soil composition (pH, nutrients, organic matter, and texture) at Van Long Nature Reserve? Soil analysis will test the assumptions that limestone soils are highly alkaline, contain toxic levels of calcium, and are sandy and porous. The expectation is that these characteristics contribute to low plant diversity and highly defended plants. Soils at VLNR are predicted to be proportionately higher in carbon than nitrogen, which would allow a greater investment in carbon-based (digestion-reducing) defenses than in nitrogen-based (toxic) defenses by plants.

3. What are the effects of plant primary and secondary constituents on *Trachypithecus delacouri* feeding selection? I wanted to determine how protein, fiber, and phenolics (especially tannins) correlate with langur food choice. The first hypothesis to be tested is that langurs will select plant parts that are lower in defensive compounds (tannins and phenolics) compared to nearby non-selected foods. The second hypothesis is that langurs will select plant parts that are lower in fiber than nearby non-selected foods. Further, langurs are expected to eat leaves that have higher amounts of protein than non-selected leaves. Building on the first and second hypotheses, the third hypothesis is that langurs will select leaves with the highest protein to fiber ratio.

4. What substrates and positional behaviors (postures and locomotions) are used by langurs to access feeding resources? Is the degree of rock climbing and locomotion of Delacour's langurs reflected in their morphology? Given the location of food sources across a wide landscape and often on the ground and rock walls, it seems reasonable to expect that these primates will spend more time (as a percentage of locomotor time) traveling terrestrially to get at these sparse resources. What is unknown are specific numbers on the variety of substrates these animals are willing to forage on and the percentage of time spent on each. Collecting such data will inform critical questions about locomotor flexibility in langurs and specific morphological adaptations to different substrates and locomotor frequencies like those described by Fleagle (1977a) for *Presbytis*. Descriptive locomotor data can also be used to assess the usefulness of the term 'semibrachiator' in Asian langurs and the relationship between body size and locomotion.

1.2 Outline of Dissertation

Following this introduction, Chapter 2 provides the theoretical basis of primate flexibility and adaptation, folivore feeding ecology and food choice, the influence of soil chemistry on vegetation, and colobine locomotor behavior. Chapter 3 provides information on the study site and study population, as well as brief and general descriptions of the behavioral observation, ecological sampling, and chemical testing methods used. In Chapter 4, the vegetation structure of Van Long Nature Reserve's Dong Quyen Mountain is described, as well as the habitat's annual phenological and weather patterns. Chapters 5, 6, 7, and 8 are the main data chapters and as such they are structured differently from the previous chapters. Chapter 5 describes the langurs' diet by food species and plant part. The temporal variation in food consumption is also depicted as is the role of limestone endemic plants in the langurs' diet. In Chapter 6, the soil composition of Dong Quyen Mountain and the chemical profiles of eaten and non-eaten plant foods are described and compared with other Asian and African colobines. In Chapter 7, activity budgets for each age and sex class are given. In Chapter 8, the positional behaviors and substrates employed are described. In addition, how the langurs' locomotor behaviors are reflected in its morphology is discussed. Finally, in Chapter 9, the findings are summarized and the conclusions reached in this dissertation are reviewed, and how they impact current understanding of limestone langur natural history generally and Delacour's langur conservation specifically is discussed.

2. Background

2.1 Primate Ecological Flexibility and Adaptation

Lack of morphological specialization coupled with increased cognition and dexterity allows primates to respond to environmental change with creative and varied behaviors (Jouffroy and Lessertisseur, 1979). Behavioral flexibility within a given species allows for even greater diversity and local adaptation; what one group occupying a specific habitat is doing might not adequately represent the species as a whole (Chapman et al., 2002a). The sampling of new foods by *Alouatta palliata* helps maintain a diverse gut flora, allowing them an adaptive mechanism for environmental change (Glander, 1975), although the same species is ineffective on any one plant defense (Glander, 1977). Similarly, colobines can induce their gut flora to adjust and handle a range of secondary metabolites in small amounts, allowing dietary flexibility. However, colobines are vulnerable to dietary change because the foregut-located microbes are not buffered by the acidic defenses of the stomach. Whatever colobines ingest goes directly to the gut microbes (Kool, 1992). The colobine fermentation chamber is also vulnerable to the ingestion of simple sugars, which can cause gut pH levels to fall, killing the symbiotic microbes (Waterman and Kool, 1994). For this reason, folivorous primates can shift to seeds when suitable leaves are scarce (Bennett, 1984; McKey, 1978; Davies, 1984) but not to sugary fruit.

The cheek-pouched monkeys, Cercopithecidae, are usually considered more flexible than the Colobinae. The flexibility that frugivores, such as *Macaca*, show in shifting from different parts of vegetation in seasonal habitats may be preadaptive for more permanent environmental changes (Chivers, 1991). Struhsaker (1978) calls *Procolobus badius* and *Colobus guereza* specialists, with dietary specializations that allow them to exploit mature forests and colonizing areas, but limits the types of habitats available to them. While multichambered stomachs allow colobines to exploit a food source (mature leaves) that is unavailable to primates with simple stomachs (Struhsaker and Leland, 1987), frugivorous macaques have the most flexible range of tenable habitats. The ability to use fermentation to detoxify secondary compounds gives colobines an advantage over cercopithecines in eating toxic substances, but the disadvantage is that eating these substances makes colobines vulnerable to bacteriostatic compounds that can inhibit gut microbe activity (Kay and Davies, 1994). For example, the dipterocarps of Southeast Asia contain terpenes with bacteriostatic resin, so although they are abundant they are rarely eaten by Asian colobines (Waterman et al., 1988).

Colobines do show considerable dietary flexibility, however, as they are able to digest fruit parts, seeds, leaf parts, flowers, and animal matter effectively (Kay and Davies, 1994; Waterman and Kool, 1994). The colobine potential for behavioral flexibility is extended due to their forestomach fermentation. Gut microbes allow derivation of energy from the cell walls of leaves, and might also help with (be primarily adapted for?) processing the chemical defenses of plants (Oates, 1987). Behavioral and physiological adaptations therefore allow colobines to live and eat in a chemically hostile environment (Waterman and Kool, 1994). Both actions might allow colobines to exploit habitats that are off limits to the monogastric cercopithecines.

2.2 Adaptation and Flexibility

Researchers measure adaptation by studying behavioral changes that are allowed through morphology and/or physiology and ultimately genetics (Lee, 1991). While once thought to occur only over time scales of millions of years and to induce small changes, adaptive change can be both rapid and major (Albertson et al., 1999; Grant and Grant, 2000). According to Fleagle (1999), adaptation is both a characteristic enabling survival as well as a process of change that enables an organism to survive in an environment. Futuyma (1998) calls it simply “improvement in function” (4), while Morbeck (1979) notes adaptive adjustments are biobehavioral. Andrewartha (1961), however, notes that adaptation is not synonymous with acclimatization. Adaptation refers to genetic differences that are irreversible except by the same evolutionary processes through which they were selected, whereas acclimatization is the reversible physiological change that an organism undergoes during its life.

Adaptation is not a monolithic term nor is it used monolithically. Gomberg et al. (1979) note the different ways primate researchers employ the term, from the broadest sense of survival and reproduction, to the narrow adjustments made in response to specific stressors. Prosser (1986) discusses three types of adaptation: genetic, environmentally induced, and ontogenetic. Environmental and developmental adaptations are possible only within genetic constraints, and so the ability to live in an environment not occupied by ancestors indicates adaptive evolution has occurred. The time scale of responses is immediate (days or weeks) for acclimatization and long-term (years or millennia) for genetic. His discussion is cogent, and yet where he calls the immediate process a short-term adaptation, Andrewartha (1961) calls it acclimatization, the word Prosser uses himself. Futuyma (1998) also notes that phenotypic adjustment (or physiological accommodation) is just one of three meanings of adaptation.

Adaptation versus accommodation or flexibility is therefore a potentially confusing argument of semantics if terms are not defined precisely. For example, in response to habitat degradation, *Rhinopithecus bieti* demonstrated ecological flexibility by adjusting its ranging patterns (Xiao et al., 2003). According to Fleagle's (1999) definition, this ecological flexibility is both adaptive and an adaptation. Potts (1998) calls the ability to survive during periods of instability "adaptive versatility," a term for which flexibility could be substituted. Studies of reproductive potential further illustrate this point. Data show that ovarian function in adult women is based on exposure to the environmental resources and stressors of pre-adult development (Vitzthum, 2001). Vitzthum's (2001) perspective explains why a robust Polish woman's fecundity would be affected by seasonal physical labor, whereas an arguably undernourished woman in Bangladesh is reproductively capable. Is this scenario describing an adaptive process or ecological flexibility? Does it matter which term is used? Tattersall (1999:115) argues that, while adaptation is a central concept for evolutionary biology, it is, "much more often than we like to admit, something we simply assume."

Adaptation has been described as a burdensome concept and one that should be used sparingly (Williams, 1966). Phylogenetic inertia can obfuscate the function of present traits, making it unclear whether traits afford an organism advantages or if traits exist as part of a species' past (Waser, 1984). Arguments using adaptation have also been critiqued for assuming that natural selection produces optimally designed animals (Gould and Lewontin, 1979). The problem with optimization theory is focusing on what individuals are supposed to do, rather than what individuals actually do. Adaptation need not be optimal. To be evolutionarily successful, an animal must survive, must reproduce, and must have offspring that survive and reproduce. Any trait or process produced by natural selection that helps an animal to survive and reproduce within an environment is adaptive, regardless of optimality.

Feeding and access to food (including locomotion) are two of the most important ways that animals adapt to and survive within their environment, directly and indirectly influencing almost all activities of an animal's day (Thorington, 1970; McMahon, 1975; Rodman and Cant, 1984; Fleagle, 1985; Chivers, 1991). Foraging is labile, optimized by the constraints set by an animal's body size and digestive physiology, and therefore at the very heart of an organism's ability to exercise ecological flexibility (Waser, 1984).

2.3 Feeding selectivity, Plant Chemistry, Soils, and Foraging in Primates

2.3.1 Feeding Selectivity and Plant Chemistry

Herbivores are commonly thought of having access to a vast resource. However, despite the abundance of green foliage in the world, many leaves are inedible. Tropical leaves defend themselves against herbivorous attack by low nutritional quality, greater toughness, and more types and amounts of secondary compounds than leaves of temperate forests (Coley and Barone, 1996). Consequently, folivorous primates must be selective in their feeding decisions (Glander, 1982). Although it makes sense to assume that limestone habitats pose distinct challenges to herbivore foraging ecology, there is no empirical evidence to illustrate how the nutritive and chemical constituents of plants on limestone soils influence foraging decisions.

Nutritional scientists and ecologists have long sought to determine relationships between the resources available in an animal's habitat and the resources actually consumed (Cornell and Hawkins, 2003; Koricheva et al., 2004; Dearing et al., 2005). All plants are not potential food items, evidenced by selective feeding in a range of herbivorous mammals (Bryant and Kuropat, 1980). Herbivores make daily feeding choices to balance nutritional requirements with secondary compound presence

(Freeland and Janzen, 1974; Glander, 1975; Waterman and Kool, 1994), but they are bound in their selection by what the environment provides. Soils are a major factor in determining an environment's vegetation and therefore in determining the flora available to herbivores. While there have been many theories proposed to account for feeding selection, there are currently two major schools of thought.

First: Coley (1983) stated that the level of fiber (and the leaf toughness associated with fiber), rather than phenolic levels, is the most important factor in herbivore food choice. In primates, leaf choice does correlate with a high protein to toughness ratio (Milton, 1982; Milton et al., 1980; Dominy and Lucas, 2001), and mature leaf protein-to-fiber ratio is a good indicator of colobine biomass in both Africa and Asia (Davies, 1984; Waterman et al., 1988; Chapman and Chapman, 2002; Chapman et al., 2002b). On the other hand, Bryant and Kuropat (1980) showed that secondary compounds control palatability and preference of beaver, grouse, and snowshoe hare foods more than do energy, fiber, or nutrient quality. Rhoades' (1985) suggestion that both nutritive and defensive compounds are important in influencing food choice seems to be more balanced and reasonable, and I focus on both of these in this study. Whether the importance of nutrition or secondary compounds is championed in feeding choices, there is overwhelming evidence that the availability of a habitat's resources dictates how much energy plants can allocate to either their primary (nutrient) or secondary (defensive) compounds.

Second: The resource availability hypothesis states that plants are expected to make a cost-benefit analysis between growth and defense based on available resources in the soil (Coley et al., 1985). Since escape from herbivory involves using nutrients to allocate energy into either growth or defense (Bryant et al., 1983; Coley et al., 1985), environments high in soil nutrients grow plants faster with lower levels of defenses. These plants can easily replace lost tissue, whereas tissue lost in nutrient-poor habitats is more difficult to replace and therefore should be more highly defended. Limestone is a resource-limited environment, challenging in terms of the edaphic and resulting vegetative communities. Further, the exposure of limestone rock and steep cliffs force colobines to travel across and up difficult substrates to access food. Limestone soils tend to be thin and highly alkaline, with limited surface water, toxic levels of calcium and/or limited availability of iron and manganese (McAleese and Rankin, 2003). Southeast Asia and China have one of the most extensive karst systems in the world with more than two million square kilometers of limestone karst combined (Laverty, 1980), yet little is known about the feeding ecology of herbivores in this environment (Dennis and Aldhous, 2004; Liu et al., 2004; Sweeting, 2004).

2.3.2 Feeding Selectivity, Plant Chemistry, and Soils

Soils are a major determining factor of plant communities (John et al., 2007). One specific aim in this project is determining the resource availability in these limestone soils. Poor soil environments are those high in sand, low in pH level, and low in mineral nutrients (Oates et al., 1990; Marquis, 2005). Poor soils are typically thin with little surface water. Low-nutrient habitats have high amounts of carbon-based defenses and low nitrogen content (Burnham, 1984). Lack of nitrogen is especially important as it has the greatest effect on growth, with the next most limiting minerals being phosphorous and potassium (Chapin, 1980).

Soil pH does influence the diversity of plant and animal communities. The soil pH of Lope, Gabon is close to the pan-tropical average, contributing to higher plant diversity than the acidic Douala-Edea, Cameroon soil, which is as low as 2.7 in some places (Harrison, 1986). Acidic soils are toxic to roots, causing phosphorous to become insoluble, and limiting nitrogen-fixing and nutrient cycling (Gartlan et al., 1978). Such acidity causes low diversity of plant biomass along transects. In nutrient-poor environments, nitrogen levels are low yet carbon is abundant; therefore, carbon-based defenses (digestion-reducing substances) are the main type of plant defense (Rhoades and Cates, 1976). Plant defenses are typically correlated with ecosystems so that nutrient-poor sites have more carbon-based (digestion-reducing) defenses and richer sites more nitrogen-based (toxic) allelochemics (Rhoades and Cates, 1976).

Support for the resource availability hypothesis comes from kudu and impala preference for fast-growing over slow-growing species (Bryant et al., 1989). The seminal paper by Janzen (1974) presented the significance of environmental resources of soils and was based on studies along South America’s blackwater rivers. Nutrient-rich and nutrient-poor soils harbor two completely different plant communities: fast-growing plants that escape herbivory and invest little in defense, and slow-growing plants that heavily defend their tissues against herbivore attack. Pioneer species have faster growth and therefore lower fiber, phenol, and toughness, as well as thinner leaves and higher nitrogen levels (Reich et al., 1992). Animals respond to such plant species by preferentially selecting them. For example, eight of the nine plant species fed on by *Colobus guere*za in Kakamega Forest, Kenya were deciduous and one was an edge species, while evergreen trees were avoided (Oates, 1977). Herbivores living in nutrient-poor environments are especially challenged by having to choose among poor dietary options, necessitating both behavioral and anatomical specialization (Milton, 1993).

Following the work of Janzen (1974) and Coley et al. (1985), researchers have sought to explain feeding ecology by the chemical and nutritional composition of vegetation. Plants invest in defenses to deter herbivores (namely insects) and primates must respond and react accordingly to balance daily nutritional requirements with both toxic and digestion-reducing substances. Fraenkel's (1959) landmark paper spurred ecologists into seeking theoretical explanations as to how plants defend themselves against herbivore attack. Fraenkel (1959) and Ehrlich and Raven (1964) offered classical plant defense theories. According to this well-supported idea, there exists a biochemical arms race between plants and insects. One way that insects and some mammals cope with plant defenses is through specialization on a specific chemical of one plant species, such as the koala (*Phascolarctos cinereus*) on eucalyptus leaves (Degabriele et al., 1978). Alternatively, many folivores have a generalized ability to process many types of defenses. The importance of habitat in the evolution of plant defense systems is supported by papers comparing poor soils with rich soils (Brunig, 1969; McKey et al., 1978).

In Amazonian Peru, Fine et al. (2004) transplanted red-clay specialists to white-sand soils and white-sand specialists to red-clay soils. Clay is less porous than sand and retains and transports water and nutrients more efficiently than does sand. Plants of red clay soils thrive in white sand if they are protected from insect herbivores (as Janzen (1974) had hypothesized). Conversely, white-sand specialists were out-competed in red-clay environments because of their slow growth. Protection given by scientists against insects was inconsequential for these plants because they already invest heavily in defenses. A similar project in Asia yielded nearly identical results (Marquis, 2005). On white sand soils without herbivores, clay species do better because they are investing in growth rather than expensive defenses. On white sand soil with herbivores, however, white sand species do better because they are protected. In the 1970s, 1980s, and 1990s, primatologists designed field studies that evaluated these relationships in colobines, because they specialize on plant foliage.

Soil composition has been shown to correlate with plant secondary compounds. In Uganda's Kibale National Park, generally more fertile and higher quality soils contain lower levels of leaf secondary compounds (Gartlan et al., 1980), although soil composition varies within the site (Struhsaker, 1997). McKey et al. (1978) showed that the acidic, low-nitrogen, low-phosphorous soils of Douala-Edea, Cameroon have plants with higher carbon-based defenses (phenolics) than similar vegetation of the lateritic soils in Kibale, Uganda. Colobines avoid the same abundant plant species in Cameroon (where they are chemically protected) that they feed on in Uganda, and eat more deciduous and second-growth vines and seeds (little or no chemical protection). At Douala-Edea, *Colobus satanus* choose leaves that are high in nutrients and low in digestion-reducing substances, and they choose seeds over leaves because of their high nutrient and lower digestion-reducing properties (McKey et al, 1981).

Oates et al. (1990) compared data from old secondary forest in Tiwai Island, Sierra Leone with two sites in Africa (Douala-Edea, Cameroon, and Kibale, Uganda) and three Asian sites (Kuala Lompat and Sepilok, Malaysia and Kakachi, India) to test the hypothesis that soils are the major determinant of primate, especially colobine, biomass. Soils from Tiwai Island were high in sand and low in pH and mineral nutrients, and mature leaves contained higher levels of condensed tannins than any site except Kibale. However, the plants from Tiwai Island also had higher than average protein content, lower than average fiber levels, the highest tannins of any of the sites, and one of the highest primate biomass levels reported anywhere; all of which led Oates et al. (1990) to conclude that soil alone is not the only environmental factor determining primate biomass. They suggest tannins and nutrient-poor soils might actually be of little consequence to primate and/or colobine biomass. McKey (1978) and Maisels et al. (1994) contradict Oates et al. (1990), stating that soil quality has a direct effect on the distribution and abundance of primate populations.

The foraging ecology of colobines or other herbivorous mammals on limestone soils has received little attention. Limestone has an extremely high amount of calcium and proportionately more potassium than other sedimentary rock (Whitmore, 1990), creating alkaline soils averaging pH of 7.0 (McAleese and Rankin, 2003). Many plants cannot grow on limestone soils, due either to the high alkalinity, toxic levels of calcium, and/or limited availability of iron and manganese (McAleese and Rankin, 2003). As a criterion to divide vegetation types, limestone soils are characterized as atypical and especially thin (Whitmore, 1990). Vegetation on karst is notoriously stunted, with many grasses, shrubs and small trees (Li et al., 2003; Day and Chenoweth, 2004; Liu et al., 2004; though see Clements et al., 2006). Limestone studies are few, but what is available suggests that limestone has a richness of endemic plants and is an especially fragile substrate (Urich, 1989; Huang et al., 2000; Li et al., 2003).

Researchers have recorded the species of limestone plants consumed by limestone langurs (*Trachypithecus francoisi* and *T. p. leucocephalus*) in China as well as the vegetation found in langur habitat ranges, but analyses of soils and of the influence of plant chemical and nutritive constituents on langur food choice have not been done

(Huang et al., 2000; Li et al., 2003; Li and Rogers, 2005). In China, *T. p. leucocephalus* licks karst rock surfaces, either to obtain nutrients or insects (Li et al., 2003). Thus, what they eat is known, but not why these choices are made. A specific aim of this project is to determine the effect of plant primary and secondary constituents on *Trachypithecus delacouri* feeding selection.

2.4 Foraging and Locomotion

2.4.1 Locomotion and Postural Behavior

Like feeding data, information on positional behavior (postures and locomotions) is fundamental to adaptive radiations as primates must access potential food items, avoid predators, and exploit their habitat (Prost, 1965; Ripley, 1967; Ripley, 1979; Rodman and Cant, 1984; Dagosto and Gebo, 1998). Despite a very small amount of time spent locomoting (Rose, 1979), locomotion is important in colobine foraging not only because an animal must find and locate food, but because it must do so efficiently. Knowledge from positional behavior elucidates the relationship between locomotion and morphology and the influence of the environment and morphology on locomotion (Doran, 1992) which also allows inferences of locomotor adaptations in the fossil record (Doran, 1993b). Positional behavior studies conducted on free-ranging primates, therefore, seek to understand the relationship between form and function in the environment in which the adaptations evolved (Bock and von Wahlert, 1965; Cant, 1992).

The definitions of locomotion and posture make them mutually exclusive terms (Prost, 1965). Locomotion requires an animal to move itself from one position to another, while postures are non-mobile (Prost, 1965). The difference between postures and locomotions, therefore, need not be energy expenditure. For example, an animal can exert energy in a flexed hanging position, but that position would be a posture if the animal was not moving (Prost, 1965). Positional behavior studies have focused more on locomotions than postures, because it has been assumed that locomotions are under a stronger selective pressure (McGraw, 1998a), but one could argue that maintaining daily sitting postures without falling out of a tree is just as important to an animal's survival as employing rare swift and powerful locomotions to escape a predator (Rose, 1973).

Positional behavior studies have aimed to relate locomotion to body size and to other habitat variables in an arboreal environment (Ripley, 1967; Fleagle and Mittermeier, 1980; Cant, 1992; Gebo and Chapman, 1995a). Larger primates have been predicted to leap less, climb more, and use larger supports than smaller primates, who were expected to leap more and use the middle and upper canopy less (Gebo and Chapman, 1995a). Sympatric Surinam monkeys mostly do show these correlations with larger sized monkeys leaping less and climbing more (Fleagle and Mittermeier, 1980). Further, in accordance with increased leaping by Malaysian leaf monkeys in the discontinuous understory (Fleagle, 1978), Surinam monkeys that traveled more in the understory and lower canopy also leapt more (Fleagle and Mittermeier, 1980). But the observed pattern did not fully hold as *Pithecia pithecia* leapt more and *Saguinus midas* leapt less than expected based on body size (Fleagle and Mittermeier, 1980). Body size and locomotion predictions were also not supported by sympatric cercopithecids in Kibale, Uganda, where the largest monkeys leapt the most and climbed the least (Gebo and Chapman, 1995a). A wider range of data across primate taxa is needed.

Despite receiving less research attention compared to suspension, vertical clinging and leaping, and bipedalism, quadrupedalism is the most common locomotor pattern in primates, especially among the Old and New World monkeys (Rose, 1973). Pronograde quadrupedalism - one of the earliest forms of primate locomotion - is today the most common locomotor category among the order (Napier, 1967; Cant, 1988). The overall quadrupedal (including running, leaping, and climbing) abilities of colobines surely permit the flexibility to transfer between the ground (including rocks) to trees and trees to ground, a substrate shift that would be difficult for a primate with a vertical clinging and leaping locomotor repertoire (Chivers, 1991). But colobines have not always been considered just arboreal and terrestrial quadrupeds. Napier and Napier (1985) categorized colobines as semi-brachiators, remarking that both New and Old World Monkeys are “quadrupeds given to arm-swinging” (47), a locomotor classification that has been contentious and ambiguous for decades.

For more than 40 years there have been problems relating anatomy to locomotor behavior patterns in the colobinae. Based on an analysis of shoulder morphology, Ashton and Oxnard (1964) first classified colobines as semibrachiators, despite qualifying colobines as quadrupedal on the ground. Based on fieldwork in Ceylon, Ripley (1967) responded by showing that the anatomical classification of colobines as semibrachiators did not square fully with behavioral data, an observation supported by additional studies of colobine positional behavior in Asian (Fleagle, 1977a, 1977b; Ripley, 1977; Fleagle, 1978) and African (Gebo and Chapman, 1995a, 1995b; McGraw, 1996, 1998a, 1998b) natural environments. Ripley (1967) also noted the ambiguity of a method that classified colobine locomotion differently for hindlimb versus forelimb behaviors and for arboreal versus terrestrial contexts.

2.4.2 Unexpected Locomotion in Asian Colobines

Captive studies in Vietnam have recently reopened and reevaluated the semibrachiator debate for Asian colobines by showing that red-shanked douc langurs (*Pygathrix nemaeus*) engage in higher than expected amounts of forelimb suspend postures and forelimb swings (Byron and Covert, 2004; Workman and Covert, 2005; Wright et al., 2008a). With 46% of all locomotor bouts being suspensory, the red-shanked douc langur (*Pygathrix nemaeus)* may be aptly called a semibrachiator, intermediate between the highly quadrupedal *Trachypithecus delacouri* (which used only non-suspensory locomotion during Byron and Covert's (2004) study) and the brachiating white-cheeked gibbon (*Hylobates leucogenys)*. Wright et al. (2008a) corroborated and added to Byron and Covert's (2004) findings by showing that the grey-shanked douc langur (*Pygathrix cinerea*) uses suspensory locomotions even more than *Pygathrix nemaeus*.

Field studies in the 1970s on arboreal Asian colobines showed that the dusky leaf monkey (*Trachypithecus obscura*) and banded leaf monkey (*Presbytis melalophos*) of Malaysia were predominantly quadrupedal with tremendous leaping abilities (Fleagle 1977a, b, 1978). These results supported those by Ripley (1967) on the Hanuman langur (*Presbytis entellus*) in Sri Lanka. Yet while *Presbytis entellus* has long been recognized as at least also partly terrestrial, the paucity of subsequent locomotor field studies on other Southeast Asian langurs allowed for the logical yet incompletely true assumption that arboreal quadrupedalism was the dominant locomotion of other Asian colobines. Hanuman langurs live in a different environment than that of the understudied rainforest langurs of Southeast Asia. Suspensory behavior and terrestriality had not been observed in forest-dwelling langurs, and in the absence of data, the genus *Trachypithecus* is described in authoritative texts as wholly arboreal (Napier and Napier, 1985). If mentioned at all, *Trachypithecus delacouri* is described as arboreal (Rowe, 1996).

Field and captive-based studies within the past few years have begun to reveal unexpected locomotor diversity among Asian primates. The odd-nosed monkeys (*Rhinopithecus, Pygathrix, Nasalis* and *Simias*) are not only arboreal quadrupeds capable of acrobatic leaping. Researchers in China have identified *Rhinopithecus bieti and R. roxellana* as traveling at least partially terrestrially (Wu, 1993; Kirkpatrick, 1996; Tan and

Poirier, 1998; Grueter et al., 2009a). In a captive setting where enclosures are nearly identical, *Pygathrix nemaeus* uses a higher percentage of suspensory postures and locomotion than do *Trachypithecus delacouri* and *T. laotum hatinhensis* (Workman and Covert, 2005). Published and anecdotal data from the field, however, have suggested that *Trachypithecus delacouri*, and other limestone species of *Trachypithecus,* are more than arboreal quadrupeds.

Both *Trachypithecus poliocephalus leucocephalus* and *T. francoisi* spend time traveling terrestrially on the exposed rocks of their limestone habitat (Li et al., 2003; Huang et al., 2003; Li and Rogers, 2005). In a habitat where cliffs comprise 10-20% of the total area, *T. p. leucocephalus* spends about 70% of its locomotor time on rocks and cliffs, with 25% on cliffs and half of all locomotion on rocks (Huang and Li, 2005). *Trachypithecus p. leucocephalus* prefers continuously forested areas (Li et al., 2003), but will run on the ground between karsts when humans are not present (Li and Rogers, 2005). Huang and Li (2005) suggest that the physical characteristics of limestone hills encourage terrestrial travel, and they propose terrestrialism as an adaptation for this habitat. Whether the amount of climbing and terrestrialism on rocks is the result of an evolutionary adaptation in this environment or a recent flexible response to current conditions is not known.

Personal observations on three other limestone langur taxa reveal rock-traveling (what has been described as terrestrial) behavior. *Trachypithecus poliocephalus* and *T.*

delacouri travel on rocks and climb cliffs in the few remnant limestone karst hills where they exist. In Vietnam's Phong Nha-Ke Bang National Park, *Trachypithecus laotum hatinhensis* travels mostly through the trees during the day, feeding in the valleys between limestone karsts. In the evenings, however, the langurs employ cliff climbing and 'terrestrial' (on rocks) locomotion to access sleeping shelters: caves or rock hangs. In a rescue center in northern Vietnam, a group of *Trachypithecus laotum hatinhensis* live on a limestone hill in a semi-wild enclosure where they travel and sit on the exposed rocks beneath the forest. That limestone langurs come to the ground, even when trees are available, suggests not only that the limestone langurs are not completely adverse to ground travel (in the absence of predators), but that they might be receiving some benefit on the ground. Benefits might include cooling themselves on rocks of lower temperature, drinking standing water in rock crevices, or licking nutrient-laden lichen from the rocks.

For the karst-living limestone langurs, small-diameter trees, an abundance of climbers and shrubs, and many exposed rock surfaces preclude much arboreal movement. Langurs prefer to feed and rest on the firmest portion of branches (Ripley, 1967), yet such arboreal substrates are often not as available in karst habitat, such as Van Long Nature Reserve, Vietnam. Fusui Precious Animal Reserve, Guangxi, China and VLNR have much exposed rock and stunted vegetation, which might serve as the firmest, and therefore preferred feeding places. At VLNR the langurs mostly sit on rocks and pull branches or vines towards themselves for the very reason that plants are not adequate supports. Resting on these rocks, however, would vary seasonally, as rocks heat up very quickly (Huang et al., 2003; personal experience), making them hot and non-preferred resting substrates in the summer. Further, while a diameter of ten centimeters at breast height is the standard used for ecological marking, Li et al. (2003) use 1.2 cm as their marker for trees and woody lianas, because monkeys are observed in trees of this size (Li, 1993). A diameter of ten centimeters is irrelevant at VLNR, because most plants have a diameter less than half that size and several plants are lianas without trunks (Chapter 4). The available substrates at VLNR are restricting some positional behaviors and use of some support types and encouraging others.

From an evolutionary perspective, the encouragement of terrestrial travel due to lack of usable substrates has support. When the savannah increased during the Miocene and forests shrunk, Old World Monkeys became more terrestrial (Chivers, 1991). Some fossil colobines, such as *Dolichopithecus,* were also quite terrestrial, perhaps for similar reasons: they used the ground due to a lack of suitable arboreal substrates (Delson, 1994). *Chlorocebus aethiops* has been in the process of making a shift from the trees to the ground, which has been quickened by the rate of deforestation and land conversion to agriculture (Napier and Napier, 1985). A similar process might be occurring for the limestone langur species that are losing the heavily forested parts of their habitat, forcing them into the rockier habitats which are less desirable to humans for agriculture (though see Clements et al., 2006), and necessarily increasing terrestriality. Rocky terrain has been cited as one of the habitats conducive to terrestrial travel (Napier and Napier, 1985). Morphological possibilities for locomotor behaviors can be tested in captivity, but *habits* (as defined by Prost, 1965) are best field-tested to determine species-specficic behavior. Given these considerations, a specific aim of this study is to determine what substrates and positional behaviors langurs use to access their food items, how this behavior is correlated to their morphology, diet, and habitat, and to compare the Delacour's langurs with other African and Asian colobines.

2.5 Trachypithecus delacouri and the Limestone Langurs

2.5.1 Taxonomy and Distribution

The Asian colobines are comprised of seven genera, with about 90-95 taxa (Nadler et al., 2002). First described by Reichenbach in 1862, *Trachypithecus* is the most widespread Asian langur genus with 15-17 species (Nadler et al., 2002). Termed the 'limestone langurs' in 2004, six taxa of the genus *Trachypithecus* are restricted to a region east of the Mekong River and north of the 17th parallel in Northen Vietnam, Laos, and Southern China (Groves, 2004; Table 1; Figure 1). These six limestone taxa form a monophyletic group, yet like many Asian primates, there is not consensus regarding their taxonomic status.

Table 1: Six limestone langur taxa of Southeat Asia

Latin Name	Common Name	General Distribution	Body size (kg)[1]	Conservation Status[2]
Trachypithecus poliocephalus	Cat Ba langur	Cat Ba Island, Vietnam	6.9	Critically Endangered
T. francoisi	Francoisi's langur	Southern China, Northern Vietnam	9-9.5	Endangered
T. p. leucocephalus	White-headed langur	Southern China	8.6	Critically Endangered
T. delacouri	Delacour's langur	Northern Vietnam	8.2	Critically Endangered
T. laotum	Laos langur	Eastern Laos	Data not available	Vulnerable
T. laotum hatinhensis	Hatinh langur	Eastern Laos, North-Central Vietnam	7.9	Endangered

[1] *T. poliocephalus*: Tilo Nadler, personal communication; *T. francoisi*: Smith and Yan Xie, 2008; *T. p. leucocephalus:* Brandon-Jones, 1995; *T. delacouri* and *T. laotum hatinhensis*: Nadler et al., 2002.

[2] *T. poliocephalus*: Bleisch et al., 2008c; *T. francoisi*: Bleisch et al., 2008b; *T. p. leucocephalus:* Bleisch et al., 2008a; *T. delacouri*: Nadler et al., 2008; *T. laotum*: Timmins et al. 2008; *T. laotum hatinhensis*: Xuan Canh et al., 2008.

Both *Trachypithecus delacouri* and *Trachypithecus poliocephalus leucocephalus* were once regarded as a subspecies of *Trachypithecus francoisi* (Wang et al., 1997). *Trachypithecus francoisi, T. delacouri*, and *T. laotum hatinhensis* are recognized as the only three 'clear' species by Brandon-Jones et al. (2004), despite the third being a subspecies. Brandon-Jones et al. (2004) also recognize *T.f. ebenus* as a separate species, while Roos (2004) classifies it as a morph of *T. l. hatinhensis*. Both *Trachypithecus francoisi* and *Trachypithecus laotum hatinhensis* sometimes have all-black morphs. The 2008 IUCN Red List reported the white-headed langur of China (previously *Trachypithecus leucocephalus*) as a subspecies of the Cat Ba langur (now *Trachypithecus poliocephalus leucocephalus*) (Bleisch et al., 2008a). This study follows Roos's (2004) classification for five limestone langur taxa: *Trachypithecus francoisi* (Francoisi langur), *T. poliocephalus* (Cat Ba langur); *T. laotum* (Laos langur) and *T. l. hatinhensis* (Hatinh langur) in the south; and *T. delacouri* (Delacour's langur), more closely related to the two southern species. For the white-capped langur of China, I follow Bleisch et al. (2008a): *Trachypithecus poliocephalus leucocephalus.* I therefore recognize four species and two subspecies in this radiation.

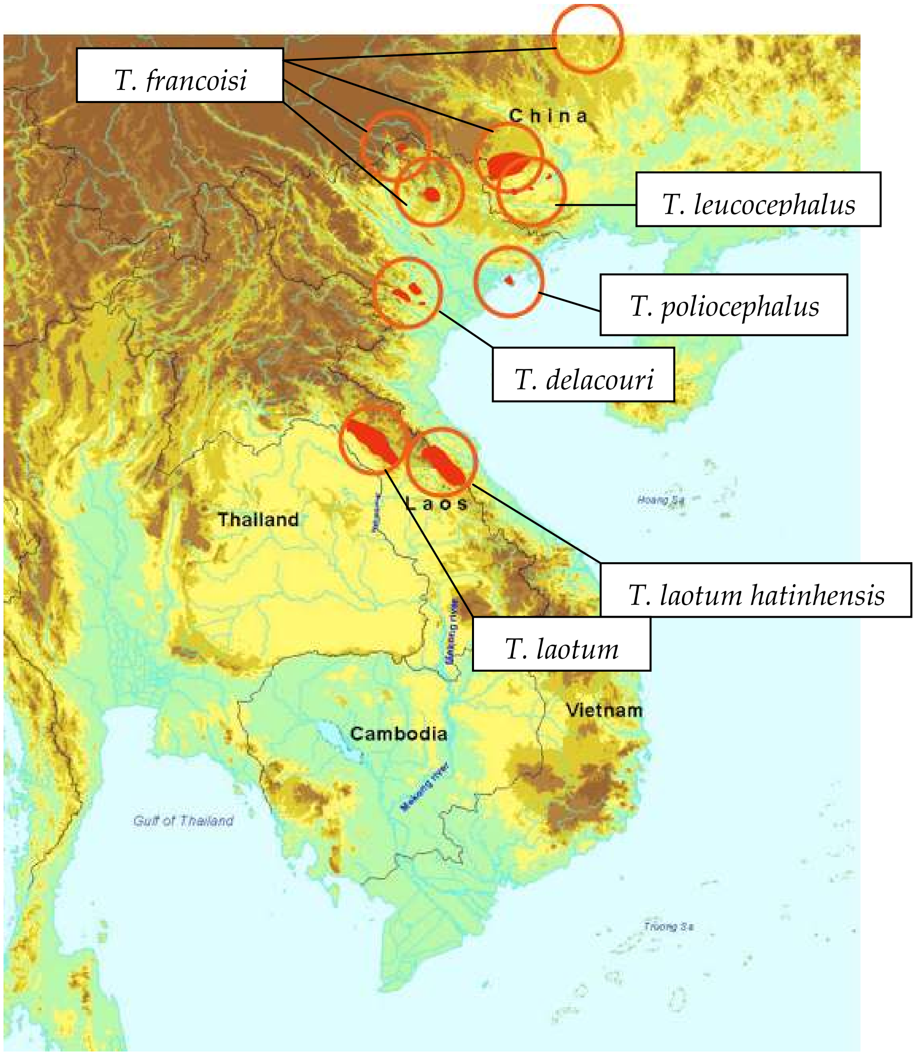

Figure 1: Distribution of six limestone langur taxa in Southeast Asia

Small population sizes and fragmented distributions are common among the limestone langurs. There are about 700-800 *Trachypithecus poliocephalus leucocephalus* remaining in the limestone hills of southeastern China (Roos, 2004) while *T. laotum* is only poorly known from Laos at this time. *Trachypithecus francoisi* is the most widespread species, with 3,200-3,500 individuals living mostly in China, and some very isolated populations in northernmost Vietnam numbering less than 300 individuals. About 60 *Trachypithecus poliocephalus* remain on the limestone mountains of Cat Ba Island, Halong Bay (Nadler et al., 2002). The range of *Trachypithecus laotum hatinhensis* may once have been more extensive, but it is now mostly restricted to the limestone mountains of Phong Nha-Ke Bang National Park in Quang Bing province, Vietnam and eastern Laos with a population of less than 2,000 individuals.

Trachypithecus delacouri is one of four limestone langur species found in Vietnam. The species was first described by Osgood in 1932 based on two animals collected by Delacour and Lowe in Hoi Xuan, Vietnam (Nadler, 2004). Currently, less than 200 individuals remain in 18-19 subpopulations making the species Critically Endangered and one of the world's 25 most endangered primates (Nadler et al., 2008). This estimate is a decrease from a 2004 estimate of 281-317 individuals in 19 subpopulations (Nadler, 2004). Populations occur in four provinces in northern Vietnam, comprising an area of 5,000 square kilometers, of which actual locales comprise 400 square kilometers (Nadler et al., 2004). A survey was started in 2008 to reassess the status of these remaining subpopulations.

2.5.2 Previous Research on *Trachypithecus delacouri*

Due to their fragmented and critically low population numbers as well as the difficulty of working in their habitat, all but one other study on wild Delacour's langurs have been restricted to distribution, census, and survey reporting (Fooden, 1996; Nadler et al., 2002; Nadler et al., 2004; Nadler, 1996). Feeding ecology studies have not been conducted in the wild and quantitative studies of locomotion have been done only in captivity (Byron and Covert, 2004; Workman and Covert, 2005). Besides the present study, there has been only one other project which has gone beyond survey and census reporting of wild Delacour's langurs. Nguyen Vinh Thanh and Le Vu Koi (2006) reported on the social organization and habitat use of the species in Van Long Nature Reserve.

3. Methods

3.1 Study Site, Population, and Methods

Research was conducted on Delacour’s langurs at the Dong Quyen karst mountain of Van Long Nature Reserve, Vietnam (20°20′55″N, 105°48′20″E). Several groups of Delacour’s langurs are known from survey and census data to populate the reserve, but only the groups on Dong Quyen are seen and protected well enough to be studied. Occurring concurrently with a doctoral research project by Nguyen Vinh Thanh of Hanoi University, this is the first study on Delacour’s langur behavioral ecology in the wild.

In June and July 2006, Nguyen The Cuong and I assessed vegetation structure on Dong Quyen mountain. The main study period took place from June 2007 through July 2008, during which time I collected data on langur feeding ecology and activity patterns, chemical makeup of eaten and non-eaten foods, soils, and locomotor and postural behavior and associated substrate use. I also collected phenological and weather data. In this chapter, the study subjects and general behavioral sampling methods are described. Methods specific to analyses of feeding ecology and activity patterns, sampling and chemical analysis of soils and foods, and positional behavior and substrate use are described in detail in subsequent chapters.

3.1.1 Study Site

Van Long Nature Reserve is a roughly 3,000 hectare wetland reserve in Ninh Binh Province, northern Vietnam. Created in 2001 to protect the habitat of the largest remaining subpopulation of Delacour's langurs, it is the stronghold for the species' future and the only feasible place in Vietnam this endemic species can be studied. Van Long Nature Reserve sits upon the Middle Triassic, marine formation called Dong Giao (Tien et al., 1991). Dong Giao is composed of light-gray massive limestone between 250 and 550 meters thick, and dark-gray thin-bedded limestone from 400-450 meters thick (Khuc et al., 2000). Van Long is located in a flat river valley, yet three-fourths of the reserve is comprised of several rugged karst mountain chains covering 1,784 hectares, for which the dominant vegetation is a mixture of mostly evergreen and some deciduous forest on limestone and arenaceous hills, of which the highest peak is 428 meters (Nguyen Ngoc Quynh, 2001). In the southeastern part of the reserve, marshes fragment the mountain ranges into separate limestone 'blocks' that rise from the water. The primary study site is one such 265-hectare block, Dong Quyen, with a highest peak of 328 meters (Figure 2).

Figure 2: Google Earth image of Van Long Nature Reserve. Dong Quyen Mountain is defined by the red border

Dong Quyen is isolated from other limestone blocks by water on its southern, southwestern, and southeastern sides and by cleared pasture along the northern and northeastern edge. At the tip of the block, at its northwest extension, a grass dam connects Dong Quyen to Hang Trang Mountain, another larger limestone block. Dong Quyen can be accessed by boat on the sides that meet water and by foot on the northeastern side that meets pasture. Dong Quyen was selected as the primary study site for this project for two reasons. First, from the outset, it was known to contain the most known langur groups within the reserve. As an ecotourism destination, langurs are regularly seen and recorded from bamboo boats by tourists and local guides (Figure 3). Second, Dong Quyen is the most accessible limestone block within the reserve for watching langurs. From a bamboo boat on the water, the entire southern and southwestern part of the block can be seen and therefore langur groups can be observed when they are in this territory.

Figure 3: Van Long's beauty and proximity to Hanoi make it a popular tourist destination

All langur groups are unhabituated and difficult to observe because on these rugged karst mountains they are too fast, shy, and excellent at climbing to follow on foot. While the langurs moved nimbly and efficiently across this habitat, limestone rock is sharp, razor-like, and can break easily, making it difficult and sometimes dangerous to negotiate. Further, there are areas of nearly 90 degree verticality that langurs can scale but are inaccessible to humans without climbing equipment. Beyond the danger, trying to follow them across the karst would be slow and unfruitful. Further, pressure from the illegal medicinal wildlife trade remains high, even in the protected area where this study occurred, and therefore habituating groups was not desirable or practical. Observing them from a boat was the most efficacious way to obtain data.

I recognize this methodology biased the feeding observations to those that could be made from the boat when the animals were in view. Compared to other non-karst colobine sites, I have comparatively few data hours over a 14 month period (372 hours). However, this is the best and only data that we have on this species' diet in the wild. I spent dawn until dusk most days of the week throughout the study period looking for langurs on my bamboo boat to get these data.

3.1.1.1 Climate and Seasonality

Northern Vietnam is characterized by hot, wet summers and cold, drier winters. From China south to 18 degrees latitude, temperatures and rainfall are seasonal (Sterling et al., 2006). The daily mean, minimum, and maximum shade temperatures were recorded at Dong Quyen Mountain during this study. Broadly speaking, a hot, wet, humid summer lasts from May to October and a less-humid, cold winter with light rain lasts from November to April. Vietnam's cold winter weather is caused by winds blowing from Siberia south to Australia, while the summer monsoon is caused by warm, wet winds coming up from the Gulf of Thailand and the Indian Ocean (Sterling et al., 2006). Late winter and early spring in the north is often characterized by a misting and light drizzle as the humidity rises. In Van Long, winter is also marked by a daily morning fog which some days covered the mountains nearly to the base.

Because there had been previously no weather data gathered at Van Long Nature Reserve, I set up a Weatherhawk Weather Station to record daily temperature, rainfall, humidity, and wind speed and direction. The weather station had a sensor that was placed in a dry place outside the ranger headquarters near Dong Quyen Mountain. The outside sensor transmitted temperature, humidity, and wind data wirelessly to a docking station that was positioned inside near a window to receive the signal. The data were transmitted every hour. The wind monitor broke within one month of the project's start and so for the rest of the project, temperature and humidity data were recorded hourly. Temperature and humidity data from the weather station were used to generate monthly means as well as monthly highs and lows. Three months into the project, the rain station broke. For the duration of the project, I measured rainfall with a rain gauge. Rainfall data are expressed as totals per month.

For analyses of seasonality, August, September, October 2007 and May, June, July 2008 are used as the wet season and November-December 2007 and February-April 2008 the dry season. Data from June and July 2007 were excluded from analyses because these months were spent learning to identify the plant species and finding groups and behavioral data collection from these months was sparse. January 2008 was also excluded from seasonality analyses, however, as very limited behavioral data exist for this month.

3.1.1.2 Fauna

Many orders of mammals are found within Van Long. Records exist for 39 species from seven orders: Insectivora, Primates, Dermoptera, Carnivora, Artiodactyla, Pholidota, and Rodentia (Forest Inventory and Planning Institute, 2001). The species list for Dermoptera and Rodentia is likely incomplete. Before Van Long was designated a nature reserve in 2001, about 4,000 goats occupied and grazed on the Van Long Mountains. A decision was made in 2004 to stop goat gazing and this decision was immediately enforced. Most goats were hunted off the mountains, including Dong Quyen Mountain. About 100 goats still illegally graze on the foothills. In addition to the Delacour's langurs, several primate taxa are found within the reserve's borders. During the study, Assamese macaques (*Macaca assamensis*) were seen periodically on Meo Cao Mountain, a limestone block that is narrowly separated from Dong Quyen by water but does not have any langurs. The slow loris (*Nyctocebus bengalensis)* occurs in Van Long.

3.1.1.3 Human Presence in the Reserve

Seven communes comprised of between 5-8 villages per commune surround Van Long Nature Reserve in the Nho Quan District: Gia Hung, Lien Son, Gia Hoa, Gia Van, Gia Lap, Gia Tan, and Gia Thanh communes. The human population is 45,000 people of the Kinh ethnic Vietnamese majority living within the buffer zone of Van Long (Dao

Nguyen, 2008). Within the 900 hectare core zone of the reserve, 17,000 people, mostly farmers, live. No one lives within the wetland or on the limestone massifs. Before 2001, people regularly entered the reserve, cutting and collecting fuelwood from the mountains and hunting langurs and other animals.

After the reserve was established, hunting and collection of forest products was banned, yet electric fishing remains an ongoing illegal activity within the reserve. The waterways maintain light human traffic, as people check daily crab-traps and collect snails. Crabs and snails are collected for personal consumption and also sold to the local market. Seasonally, vegetation along the bottom of the wetland is collected to feed pigs and small water organisms are collected. During the summer, water buffalo regularly wade into the reserve to feed. Hundreds of domestic ducks are kept within the reserve wetland and rice is seasonally planted along the southeastern base of Dong Quyen. People are not allowed to climb Dong Quyen Mountain and only once during the study period were humans seen illegally climbing the mountain. The four teenage boys who climbed the mountain were caught by a reserve guard and reprimanded.

Tourism has increased dramatically in Van Long over the past few years. In 2004, about 15,000 foreigners came to the reserve and by 2006 that number was more than 80,000. The success of tourism, the associated growth of the Van Long tourism facilities, and the nearby economic development are of concern to the local population. Tourism revenues in 2006 exceeded 1,412,095 million VND, or about $86,000. The revenue generated from tourism activities within the reserve goes to ministerial officials while the communes do not receive any of the generated revenues.

3.2.1 Study Subjects

I observed seven free-ranging groups containing from 4 to 16 individuals on Dong Quyen Mountain during the study period. In addition, one bachelor group of four males (thought to be only two males in June 2008) was observed. I saw one solo male langur in August 2007. When the study ended in July 2008, there were between 68-70 individuals living on Dong Quyen Mountain (Table 2).

Table 2: Composition of Dong Quyen langur groups in July 2008

Age-Sex Class	St6	St7	Valley	9C	East	M	WE	Total
Adult Male	1	1	2	1	1	1	2	9
Adult Female	5	5	1	8	7	2	1 or 2	29 or 30
Subadult Male								0
Subadult Female		1	1			1		3
Subadult (sex unknown)					3		2 or 3	5 or 6
Juvenile Male	1							1
Juvenile Female	2							2
Infant	6	1		6	5			18
Total	15	8	4	15	16	4	6	68

More than 80% of behavioral data come from three main study populations: St7 Group, St6 Group, and Valley Group (Table 2). When the study began, St7 was comprised of one adult male, five adult females, three juveniles (one male, two females), and two infants. Three orange babies were observed in March 2008, and one orange baby was seen in June 2008. St6 started as one adult male, five adult females, and one subadult female. One orange baby was observed in December, but it died. One orange baby was observed in May 2008. My field assistant Le Van Dung observed another baby in September 2008. Valley started as four individuals: two adult males, one adult female, and one subadult female. On March 2008, the adult female was missing and two weeks later, the subadult female was missing from the group as well. The subadult female left Valley over a period of several days. She spent time with the two adult males of Valley while also associating and feeding near a new group of one male and two adult females. At the end of the study, Valley Group was only two males.

I also collected data opportunistically on four other Dong Quyen groups (Table 2). The 9C Group was seen more regularly than any of the other additional groups. The 9C Group started as two adult males and eight adult females. In April 2008, only one adult male was observed. A likely explanation is that one of the two adult males was in fact a nearly adult male who emigrated. Six babies were born into this group over the study period: three in September/October 2007, one in November/December 2007, and two in April 2008. East Group had 16 individuals when the study ended. The adult and subadult composition in the group was unknown, but there were three babies initially and two orange babies were observed in March 2008. The group into which the Valley

Group subadult joined (M Group) was comprised of one adult male and two adult females in addition to the new subadult. I saw the WE Group once in April 2008; it was comprised of two adult males, two adult females, and two subadults.

There were three other known groups of langurs on neighboring mountains on which no behavioral data were collected. Hang Trang Mountain, which is connected to Dong Quyen by a grass dam, had a group of seven langurs. Gia Hoa commune had two groups, one of four langurs and one of seven langurs. On surveys to the northwestern portion of the reserve, Le Van Dung heard langurs but it is unclear how many live in that region, which is more forested but less protected than the Dong Quyen Mountain. I estimate the total population of langurs at Van Long Nature Reserve at 85-95 individuals.

3.3.1 Data Collection

3.3.1.1 Feeding Behavior

I collected data on adult males, adult females, females who were lactating or had dependent young, and subadults during dawn-dusk focal animal follows (Altmann, 1974), or until the group moved out of view on the mountain. Behavioral data were collected on 222 days during the study period for a total of 372 hours (Table 3). Langurs were searched for during many of the non-study days. A day was only considered a study day if behavioral data were able to be recorded. Therefore, the number of contact hours (when the locations of langur groups were identified but individuals were not seen clearly for data collection; N=476 hours) was much higher than the number of data hours (N=372 hours).

Table 3: Observations of langurs by month

Month	Hours	Days
June 07	21	11
July 07	1	8
August 07	34	22
September 07	25	15
October 07	42	22
November 07	35	22
December 07	42	21
January 08	<1	3
February 08	10	18
March 08	55	15
April 08	37	19
May 08	32	20
June 08	21	11
July 08	17	15
Total	372	222

Age and sex determination of Delacour's langurs is possible, even from a distance (Table 4). Like most Asian colobines, infants are born bright orange (Rowe, 1996), with a tassel at the end of the tail. By four months the body is black and the 'trousers' are gray. At nine months, the body turns black with dark gray 'trousers' and the head becomes light brown. By two years the gray color changes to white and the tail becomes carrot-shaped. Females have a white pubic patch. Roughly equal amounts of data were collected on adult males and adult females (Table 5) with significantly fewer data hours on subadults and females with dependent young.

Table 4: Age-sex classes used in this study*

Age-Sex Class	Description	Age estimates (months)
Orange infant	Hair completely bright yellow-orange to dark orange	0-4
Small juvenile	Hair black; parts which later change to white "shorts" are dark grey; tassel at end of tail; no difference between the sexes	4-9
Medium juvenile	Body black; "shorts" dark grey; head light brown; tassel at end of tail; no differences between the sexes	9-18
Large juvenile	Larger size than medium juvenile; few light brown hairs remain on head at start of third year; "shorts" changing from dark grey to white; tassel at end of tail	18-36
Subadult female	"Shorts" white; white pubic patch clearly visible; tail has carrot-like shape with larger diameter close to root	36-48
Subadult male	"Shorts" white; tail has carrot-like shape with larger diameter close to root; white-pink penis visible against black hair	36-60
Adult female	Full somatic growth attained (7.5 kg)	48+
Adult male	Full somatic growth attained (8.5kg)	60+

*Nadler, unpublished data; Nadler et al., 2002

Table 5: Number of hours collected on age-sex langur groups

Age-Sex Class	St6	St7	Valley	9C	East	M	14C	Solo	Totals
Males	66	32	42	2	<4	<2	<1	<10	157
Females	119	23	<4	9			<1		155
Females with infants	<2	22		16					<40
Subadult/juv	<13	<3	<6						<22
Totals	199	78	<50	27	<4	<2	<2	<10	372

All behavioral data were collected from a bamboo boat, using Canon 18x50IS binoculars and a Bushnell Trophy 20-60x65 spotting scope. Climbing on to the karst (as was done for transect monitoring and feeding sample collection) provoked alarm calls from groups followed by flight up the mountain. In addition, langurs are not fully habituated at Van Long, but will tolerate closer approach (<10 meters) by humans in the boat. On several occasions, I was able to come within 10 meters of two of the groups. These close encounters occurred when langur groups descended to the wetland to drink or when they descended to feed on climbers (especially *Ipomeae bonii*) growing on rocks along the wetland.

Behaviors were recorded in the categories of *Feed*, *Travel*, *Rest*, *Social*, and *Drink* (Table 6). It was also noted when a focal animal was *Out of View*. When a focal animal was feeding, the species and plant part (young leaves, mature leaves, unripe fruit, ripe fruit, flowers, buds, stems, and seeds) consumed was noted. When an animal was feeding but the plant item could not clearly be seen (either due to weather or lighting), the item was classified as unidentified.

3.3.1.2 Activity Budgets and Positional Behavior

I collected positional behavioral data in a similar manner as was described above for feeding. During a focal animal follow, I noted the animal's activity (*Feed, Rest, Travel, Social, Drink*) along with the substrate (rock or tree), and the specific posture or locomotion. I used Hunt et al.'s (1996) list of 118 positional behaviors (49 postures and 69 motions). I recorded each change of posture or locomotion as a bout (following the methods of Fleagle, 1976; Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995b), even if the associated activity did not change. Detailed information on positional behavior data collection is given in Chapter 8.

Table 6: Activities recorded during focal follows

Activity	*Description*
Rest	Individual standing, sitting, or lying, and not engaged in any other activity except for self-grooming
Social	Individual grooms another individual, or is recipient of grooming by another individual; OR individual plays with another individual; OR individual mounts or is mounted by another individual
Travel	All locomotion
Drink	Individual consumes water
Feed	Individual takes or moves vegetation towards its mouth, ingests, masticates, or swallows food (Fashing, 2001a)

3.3.1.3 Plant Sample Collection and Processing

I collected both eaten and non-eaten plant samples for chemical analysis. When a focal animal moved away from a feeding plant, I- along with the field assistance of Le Van Dung- climbed the karst and recorded the consumed plant's species name, the part consumed, the diameter at breast height (DBH) for trees, the GPS location, the height of the tree or shrub, the plant's height on the karst, whether the plant was growing in shade or sunlight, and by which age-sex langur category the plant was eaten (Table 7). So-called eaten plant samples were samples that came from the same phenophase of the same individual plant on which the focal animal was observed to feed. For example, if a focal female Delacour's langur was feeding on the young leaves of a *Broussonetia papyrifera* tree, then our 'eaten' sample was other young leaves from that same individual *Broussonetia papyrifera* tree. Plants were identified by Nguyen The Cuong of the Institute for Ecology and Biological Resources and Nguyen Manh Cuong of Cuc Phuong National Park.

Table 7: Ecological characteristics of plants from which feeding samples were collected on Dong Quyen Mountain

Species	**Month**	**Part eaten**	**DBH (cm)**	**Plant Height (m)**	**Karst Height (m)**	**Focal**
Vitex sp	Aug 07	YL	5.1	3	40	AF
Sample #14	Aug 07	YL	4.1	2	35	AF, AM
Broussonetia papyrifera	Aug 07	YL	8.6	4	4	AM
Ficus micocarpa	Aug 07	YL	4	3	12.7	AF
Alangium kurzii	Aug 07	ML	10.5	5	70	AF
A. kurzii	Aug 07	ML	2.9	4	64	AF
A. kurzii	Aug 07	ML	4.6	5	64	AF
B. papyrifera	Jun 07	YL	6.1	5	27.6	AF
Ficus sp	Aug 07	YL	3.8	4	30	AF
Derris tonkinensis	Jun 07	YL	NA	NA	3.1	AM
D. tonkinensis	Aug 07	YL	NA	NA	10	AF
A. kurzii	Sep 07	ML	5.7	4	37	AM
Bauhinia rubro	Sep 07	YL	NA	NA	37	AM
F. microcarpa	Sep 07	YL	6.7	3	58	AM
Maclura cochinchinensis	Sep 07	YL	NA	NA	8	AM
A. kurzii	Sep 07	YL	5.6	3	50	AM
A. kurzii	Sep 07	YL	4.3	3	22	AM
D. tonkinensis	Sep 07	YL	NA	NA	1	SF
Linociera verticillata	Sep 07	YL	2.7	2	7	SF
Sample #32	Sep 07	YL	3	2	7	SF
B. papyrifera	Oct 07	YL	7.6	3	6	AM
B. papyrifera	Oct 07	YL	2.4	3	2	SF
A. kurzii	Oct 07	YL	5.9	4	21	AM
Ficus sp	Oct 07	YL	8.8	3	40	AM
Gardenia tonkinensis	Oct 07	YL	4.5	2	13	AF
Lantana camara	Oct 07	UF	NA	NA	10	AF,AM
sample #39	Oct 07	YL	4.5	2	5	AF

Table 7, continued

Ipomoea bonii	Oct 07	YL	NA	NA	1	AF
B. papyrifera	Oct 07	YL	5.9	5	22	AM
Sample #42	Oct 07	YL	5.7	3	5	AF
Alchornia tiliaefolia	Oct 07	ML	4.6	4	16.3	AF
G. tonkinensis	Nov 07	ML	5.6	4	5	AF
G. tonkinensis	Nov 07	YL	3	4	5	AF
Diospyros mollis	Nov 07	ML	8.8	6.5	101	AF, AM
I. bonii	Nov 07	YL	NA	NA	1	AF
Zanthoxylum sp	Nov 07	YL	NA	NA	10	AF
B. papyrifera	Dec 07	YL	5.6	3	2	AM
Diospyros mollis	Feb 08	ML	4.1	4	65	AM
D. tonkinensis	Feb 08	ML	NA	NA	2	Afb
F.microcarpa	Feb 08	YL	7	2	41	AF
Wrightia macrocarpa	Apr 08	YL	6.5	4	44	AF
F. microcarpa	Apr 08	YL	17.2	3	82	AF
W. macrocarpa	Apr 08	YL	6.2	2	86	AF
Mallotus philippensis	May 08	ML	1.3	1	4	AF
L. verticillata	May 08	YL	1.8	3	8	AF
Combretum griffithii	May 08	YL	NA	NA	8	AF
D. tonkinensis	May 08	YL	NA	NA	8	AFb
A. kurzii	May 08	YL	2.5	2	30	AF
G. tonkinensis	May 08	YL	5.6	2	10	AF
W. macrocarpa	May 08	YL	3.2	2	30	AF
B. papyrifera	May 08	YL	3.2	2	4	AF

AF=Adult female; AM=Adult male; AFb=Adult female with baby; SF=Subadult female

I collected samples from morning and afternoon feeding sessions and from all sex and age groups, excluding infants. Despite my desire to collect from all parts of the habitat, there were certain parts of the Van Long environment that langurs could reach but I could not. Due to limits of accessibility imposed by karst topography, there were sometimes instances when I could see and record the species, age, and plant part being eaten, but I could not collect a plant sample.

Samples were weighed, dried in the shade over a period of days or weeks (depending on weather), and then kept at room temperature until analysis. Samples were analyzed for crude protein, neutral detergent fiber (NDF), condensed tannin, total phenolics, crude ash, and water content at 1) Food and Chemical Microbiology and Food Testing Laboratory of Quality Assurance and Testing Center Number, Hanoi; 2) National Institute of Animal Husbandry, Hanoi.

3.3.1.4 Soil Sample Collection and Processing

Soil samples were collected from along two established phenology transects within the home range of the study groups in August 2007 and February 2008. Samples were cleaned of debris, sundried, and mailed to the United States to be analyzed for pH; several extractable nutrients (Ca, Mg, K, Na, P, Zn, Fe, and Mn); total carbon; total nitrogen; carbon/nitrogen ratio; and texture (total sand, silt, and clay) at Brookside Laboratories Inc. in Brookside, OH.

3.4.1 Statistical Analyses

Behavioral data were used to generate two types of descriptive statistical data. First, an activity budget was generated to determine how much of the langurs' time was spent feeding and an activity budget was also generated for each age/sex group (Chapter 7). In addition, behavioral data were used to determine the dietary composition of langurs at Van Long as a whole and for each age/sex group (Chapter 5). Descriptive statistics were employed to show frequencies of consumed plant parts and species as well as seasonal variations and between sexes (Chapter 5). Spearman's Rank Correlation Coefficient was used to test for relationships between plant part abundance and consumption (Chapter 4). A Spearman's Rank Correlation Test was also used to test for relationships between body size and intermembral index, body size and leaping frequency (%), and intermembral index and leaping frequency (%) (Chapter 8). Differences in positional behavior bouts between age and sex groups were compared using Chi Square tests (Chapter 8).

The contributions of different food species and plant parts to the Delacour's langurs' annual feeding habits were calculated as a proportion of the total number of all feeding records (N=5,949; 108 hours; Table 8). Monthly feeding habits were calculated as proportions of the feeding records for each month. Based on rainfall results over the study period, feeding differences were compared between wet and dry seasons. August-October 2007 and May-July 2008 are used as the wet season and November- April 2008 the dry season. January 2008 was excluded from seasonality analyses, as very limited behavioral data exist for this month. Differences in plant chemistry (crude protein, neutral detergent fiber, total phenolics, condensed tannins, water, and ash content) were analyzed between several groups (Chapter 6). All differences were analyzed using a non-parametric Wilcoxon test (the equivalent of the non-parametric Mann-Whitney *U* test). All statistical analyses were performed using open software R 2.7.1 for Windows and XLSTAT 2009.

Table 8: Feeding records by month

Month	Feeding Hours	Observation Days
June 07	5	11
July 07	<1	8
August 07	9	22
September 07	7	15
October 07	12	22
November 07	12	22
December 07	13	21
January 08	0	3
February 08	3	18
March 08	12	15
April 08	12	19
May 08	9	20
June 08	5	11
July 08	5	15
Total	104	222

4. Vegetation Structure, Phenology, and Weather

In this chapter, the vegetation structure on Dong Quyen Mountain is described based on four vegetation transects. The annual phenological patterns of the habitat are also described based on two phenology transects which were monitored bimonthly. The Delacour's langurs' temporal consumption of plant parts based on this phenological availability is given. At the time the study began, the food species frequently consumed by Delacour's langurs were unknown and therefore were not monitored intentionally. In addition, the weather at Van Long Nature Reserve during the study period is described.

4.1 Vegetation Structure

During June 2006, four transects were walked in the Delacour's langur habitat at Van Long Nature Reserve to generate a species list for the Dong Quyen Mountain. Transect areas were chosen based on having langurs as well as differences in habitat (amount of sunlight/shade received, orientation to the sun, and elevation). The first transect was 308 meters and located in the home range of the Valley group. The second transect was 271 meters and located in the home range of the St6 group. The third transect was 119 meters in length and located on the backside of Dong Quyen Mountain. In 2006, blasting was occurring on a nearby mountain on this side and has since accelerated. The number of langurs or groups that used this side of the mountain was unclear in 2006 and remains unclear. The fourth transect was also 119 meters and was located in the easternmost portion of Van Long, from which a group of 12 langurs was known. The first and second transects were the basis for the phenology transects which were established in 2007 and monitored throughout the course of the project. Species name was recorded for each plant within two meters of the transects and plants were classified as climbers, shrubs, trees, grasses, or herbs. Plants were identified by Nguyen The Cuong of the Institute for Ecology and Biological Resources and Nguyen Manh Cuong of Cuc Phuong National Park.

The total abundance of plants sampled along the four transects was 283. The four transects included 37 shrubs, 84 climbers, 72 herbs, 86 trees, and 4 grasses. Trees comprise 30.4% of the vegetation, climbers 29.7%, herbs 25.4%, shrubs 13.1%, while grasses are 1.4% of the vegetation on Dong Quyen Mountain (Table 9).

Table 9: Vegetation structure on Dong Quyen Mountain

Vegetation type	% of habitat
Shrub	13.1
Climber	29.7
Herb	25.4
Tree	30.4
Grass	1.4

The four transects revealed a species richness of 145 species from 63 known plant families (Table 10). Results of the four vegetation transects are given in Tables 11-14. The first transect had 29 species not represented in the other three transects. Fourteen species were exclusive to the second transect; 26 to the third; and 14 species to the fourth transect. Five species were found in all four transects: *Desmos cochinechinensis, Iodes vitiginea, Alchornia tiliaefolia, Ageratum congzoides, and Cymbidium sp.*

Several families were represented by more than one species. The following plant families are represented by two species on Dong Quyen Mountain: Anacardiaceae, Annonaceae, Apocynaceae, Compositae, Connaraceae, Cucurbitaceae, Leguminosae-Caesalpinioideae, Myrtaceae, Oleaceae, Rosaceae, Smilacaceae, and Vittaroideae. The following plant families have three species on the mountain: Convolvulaceae, Gesneriaceae, Leguminosae-Papilionoideae, Menispermaceae, Orchidaceae, Rhamnaceae, and Urticaceae. Araceae and Rubiaceae are represented by four species on Dong Quyen Mountain, and Gramineae and Rutaceae have five species. Dong Quyen Mountain has eight species of Vitaceae and Verbenaceae, nine species of Moraceae and eleven species of Euphorbiaceae. On the Dong Quyen Mountain, the dominant families are Euphorbiaceae (7%), Alangiaceae (6.7%), Moraceae (6.1%), Verbenaceae (5.6%), Urticaceae (5%), Annonaceae (4%), Vitaceae (4%), and Araceae (3.5%). These eight families account for 42% of plants.

Table 10: Species list for Dong Quyen Mountain, Van Long Nature Reserve

Species	Family
Justicia sp	Acanthaceae
Adiantum soboliferum	Adiantaceae
Rhus chinensis	Anacardiaceae
Semecarpus tonkinensis	Anacardiaceae
Alangium kurzii	Alangiaceae
Desmos cochinchinensis	Annonaceae
Uvaria microcarpa	Annonaceae
Alyxia sp	Apocynaceae
Wrightia macrocarpa	Apocynaceae
Alocasia sp	Araceae
Amorphophallus tonkinensis	Araceae
Pothos repens	Araceae
Raphidophora decursiva	Araceae
Schefflera pes-avis	Araliaceae
Hoya villosa	Asclepiadaceae
Asplemium sp	Aspleniaceae
Impatiens verrucifer	Basellaceae
Drymaria cordata	Caryophyllaceae
Celastrus sp	Celastraceae
Quisqualis indica	Combretaceae
Ageratum congzoides	Compositae
Bidens pilosa	Compositae
Connarus paniculatus	Connaraceae
Rourea minor	Connaraceae
Merremia bimbim	Convolvulaceae
Merremia vitifolia	Convolvulaceae
Tridynamia megalantha	Convolvulaceae
Kalanchoe integra	Crassulaceae
Gynostemma laxum	Cucurbitaceae
Gynostemma pentaphyllum	Cucurbitaceae
Dracaena cochinchinensis	Dracaenaceae
Diospyros mollis	Ebenaceae
Elaeagnus sp	Elaeagnaceae

Table 10, continued	
Vaccinium sp	Ericaceae
Alchornia tiliaefolia	Euphorbiaceae
Antidesma sp	Euphorbiaceae
Bridelia sp	Euphorbiaceae
Claoxylon indicum	Euphorbiaceae
Croton sp	Euphorbiaceae
Macaranga denticulate	Euphorbiaceae
Mallotus philippinensis	Euphorbiaceae
Mallotus yunnanensis	Euphorbiaceae
Phyllanthus sp	Euphorbiaceae
Sapium discolor	Euphorbiaceae
Unknown	Euphorbiaceae
Unknown	Flacourticaceae
Chirita drakei	Gesneriaceae
Chirita hamosa	Gesneriaceae
Paraboea sp	Gesneriaceae
Gnetum montanum	Gnetaceae
Arundinella bengalensis	Gramineae
Centotheca lappacea	Gramineae
Imperata cylindrica	Gramineae
Panicum curviflorum	Gramineae
Phragmites vallatoria	Gramineae
Bambusa sp	Gramineae-Bambusoideae
Iodes vitiginea	Icacinaceae
Litsea glutinosa	Lauraceae
Leea rubra	Leeaceae
Bauhinia ornate	Leguminosae-Caesalpinioideae
Saraca dives	Leguminosae-Caesalpinioideae
Dalbergia sp	Leguminosae-Papilionoideae
Derris tonkinensis	Leguminosae-Papilionoideae
Vigna sp	Leguminosae-Papilionoideae
Fagraea ceilanica	Loganiaceae
Melastoma septemnervium	Melastomataceae
Cipadessa baccifera	Meliaceae
Stephania longa	Menispermaceae
Stephania rotunda	Menispermaceae

Table 10, continued

Tinospora sinensis	Menispermaceae
Broussonetia papyrifera	Moraceae
Ficus benjamina	Moraceae
Ficus hispida	Moraceae
Ficus pumila	Moraceae
Ficus sp	Moraceae
Ficus sp	Moraceae
Ficus sp	Moraceae
Maclura cochinchinensis	Moraceae
Streblus ilicifolius	Moraceae
Maesa perlaria	Myrsinaceae
Psidium guajava	Myrtaceae
Syzygium sp	Myrtaceae
Jasminum elongatum	Oleaceae
Jasminum longisepalum	Oleaceae
Cymbidium sp	Orchidaceae
Nervilia sp	Orchidaceae
Unknown	Orchidaceae
Oxalis corniculata	Oxalidaceae
Caryota bacsonensis	Palmae
Pandanus nanofrutex	Pandanaceae
Pyrrosia lanceolata	Polypodiaceae
Clematis granulata	Ranunculaceae
Sageretia theezans	Rhamnaceae
Ventilago sp	Rhamnaceae
Zizyphus oenoplia	Rhamnaceae
Rubus alceaefolius	Rosaceae
Rubus cochinchinensis	Rosaceae
Mussaenda sp	Rubiaceae
Paederia foetida	Rubiaceae
Randia spinosa	Rubiaceae
Psychotria sp	Rubiaceae
Euodia lepta	Rutaceae
Skimmia japonica	Rutaceae
Zanthoxylum avicennae	Rutaceae
Zanthoxylym scabrum	Rutaceae

Table 10, continued

Zanthoxylum nitidum	Rutaceae
Allophyllus sp	Sapindaceae
Lygodium conforme	Schizeaceae
Smilax perfoliata	Smilacaceae
Smilax sp	Smilacaceae
Stemona tuberosa	Stemonaceae
Sterculia lanceolata	Sterculiaceae
Camellia sp	Theaceae
Grewia asiatica	Tiliaceae
Anthrophyum callifolium	Unknown
Cycas sp	Unknown
Pachygone sp	Unknown
Pericampylus glaucus	Unknown
Sinarundinaria sp	Unknown
Unknown	Unknown
Unknown	Unknown
Debregeasia squamata	Urticaceae
Laportea interrupta	Urticaceae
Pilea peltata	Urticaceae
Callicarpa giraldii	Verbenaceae
Clerodendrum cyrtophyllum	Verbenaceae
Clerodendrum japonicum	Verbenaceae
Lantana camara	Verbenaceae
Premna balansae	Verbenaceae
Premna serratifolia	Verbenaceae
Premna stenobotrys	Verbenaceae
Vitex trifolia	Verbenaceae
Ampelopsis cantoniensis	Vitaceae
Cayratia oligocarpa	Vitaceae
Cayratia wrayi	Vitaceae
Cissus subtetragona	Vitaceae
Tetrastigma eberhardtii	Vitaceae
Tetrastigma pachyphyllum	Vitaceae
Tetrastigma tonkinense	Vitaceae
Vitis pentagona	Vitaceae
Pteris multifida	Vittaroideae

Table 10, continued	
Pteris sp	Vittaroideae
Alpinia tonkinensis	Zingiberaceae

Table 11: First vegetation transect

Species	Family	Vegetation Type
Zanthoxylum scabrum	Rutaceae	Shrub
Desmos cochinechinensis	Annonaceae	Climber
Lantana camara	Verbenaceae	Herb
Desmos cochinechinensis	Annonaceae	Climber
Macaranga balansae	Euphorbiaceae	Tree
Lantana camara	Verbenaceae	Herb
Stephania rotunda	Menispermaceae	Climber
Desmos cochinechinensis	Annonaceae	Climber
Mallotus yunnanensis	Euphorbiaceae	Tree
Pericampylus glaucus	Unknown	Climber
Ageratum congzoides	Compositae	Herb
Alchornia tiliaefolia	Euphorbiaceae	Tree
Desmos cochinechinensis	Annonaceae	Climber
Debregeasra squamata	Urticaceae	Tree
Litsea glutinosa	Lauraceae	Tree
Merremia pierrei	Convolvulaceae	Climber
Impatiens verrucifer	Basellaceae	Herb
Laportea interrupta	Urticaceae	Herb
Jasminum undulatum	Oleaceae	Climber
Stephania rotunda	Menispermaceae	Climber
Vaccinium sp.	Ericaceae	Tree
Ficus sp	Moraceae	Tree
Skimmia japonica	Rutaceae	Tree
Rourea minor	Connaraceae	Shrub
Premna balansae	Verbenaceae	Climber
Chirita hamosa	Gesneriaceae	Herb
Oxalis corniculata	Oxalidaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Croton sp	Euphorbiaceae	Shrub
Pothos repens	Araceae	Climber
Pyrrosia lanceolata	Polypodiaceae	Herb
Psychotria fleuryi	Rubiaceae	Climber
Pyrrosia lanceolata	Polypodiaceae	Herb

Table 11, continued

Alpinia tonkinensis	Zingiberaceae	Herb
Laportea interrupta	Urticaceae	Herb
Chirita drakei	Gesneriaceae	Herb
Broussonetia papyrifera	Moraceae	Tree
Ficus sp	Moraceae	Tree
Paederia foetida	Rubiaceae	Climber
Alangium kurzii	Alangiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Laportea interrupta	Urticaceae	Herb
Laportea interrupta	Urticaceae	Herb
Impatiens verrucifer	Basellaceae	Herb
Impatiens verrucifer	Basellaceae	Herb
Premna balansae	Verbenaceae	Climber
Pyrrosia lanceolata	Polypodiaceae	Herb
Adiantum soboliferum	Adiantaceae	Shrub
Paraboea swinhoii	Gesneriaceae	Herb
Centotheca uniflora	Graminae	Herb
Uvaria microcarpa	Annonaceae	Climber
Diospyros mollis	Ebenaceae	Tree
Premna balansae	Verbenaceae	Climber
Diospyros mollis	Ebenaceae	Tree
Diospyros mollis	Ebenaceae	Tree
Sageretia theezans	Rhamnaceae	Shrub
Sinarundinaria sp	Unknown	Tree
Lygodium conforme	Schizeaceae	Climber
Ficus sp	Moraceae	Tree
Schefflera pes-avis	Araliaceae	Shrub
Semecarpus tonkinensis	Anacardiaceae	Tree
Mussaenda sp	Rubiaceae	Climber
Tinospora sinensis	Menispermaceae	Climber
Justicia sp	Acanthaceae	Herb
Gynostemma laxum	Cucurbitaceae	Climber
Wrightia macrocarpa	Apocynaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Dalbergia sp.	Leguminosae-Papilionoideae	Climber

Table 11, continued

Sapium discolor	Euphorbiaceae	Tree
Vigna sp.	Leguminosae-Papilionoideae	Herb
Derris tonkinensis	Leguminosae-Papilionoideae	Climber
Stemona tuberosa	Stemonaceae	Herb
Gnetum montanum	Gnetaceae	Climber
Cymbidium sp.	Orchidaceae	Herb
Asplemium sp	Aspleniaceae	Herb
Drymaria cordata	Caryophyllaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Impatiens verrucifer	Basellaceae	Herb
Antidesma sp	Euphorbiaceae	Shrub
Alocasia sp	Aracea	Herb
Bauhinia ornata	Leguminosae-Caesalpinioideae	Climber
Iodes vitiginea	Icacinaceae	Climber
Hoya villosa	Asclepiadaceae	Climber
Tetrastigma eberhardtii	Vitaceae	Climber
Tetrastigma harmandii	Vitaceae	Climber
Ficus benjamina	Moraceae	Tree
Cissus subtetragona	Vitaceae	Climber
Premna serratifolia	Verbenaceae	Climber
Bidens pilosa	Compositae	Herb
Bidens pilosa	Compositae	Herb
Dracaena cambodiana	Dracaenaceae	Tree
Raphidophora tonkinensis	Araceae	Climber
Sterculia lanceolata	Sterculiaceae	Tree
Connarus semidecandrus	Connaraceae	Shrub
Ampelopsis cantoniensis	Vitaceae	Climber
Amorphophallus tonkinensis	Araceae	Herb
Kalanchoe blossfieldiana	Crassulaceae	Herb
Syzygium sp.	Myrtaceae	Tree
Unknown	Orchidaceae	Herb
Vitis pentagona	Vitaceae	Climber
Sterculia lanceolata	Sterculiaceae	Tree

Table 11, continued

Unknown	Flacourticaceae	Tree

Table 12: Second vegetation transect

Species	Family	Vegetation Type
Desmos cochinchinensis	Annonaceae	Climber
Laportea interrupta	Urticaceae	Herb
Laportea interrupta	Urticaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Ampelopsis cantoniensis	Vitaceae	Climber
Broussonetra papyrifera	Moraceae	Tree
Allophyllus sp	Sapindaceae	Shrub
Ageratum conzyoides	Compositae	Herb
Laportea interrupta	Urticaceae	Shrub
Laportea interrupta	Urticaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Unknown	Euphorbiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Mallotus philippinensis	Euphorbiaceae	Tree
Bauhinia ornata	Leguminosae-Caesalpinioideae	Climber
Cayratia wrayi	Vitaceae	Climber
Alchornia tiliaefolia	Euphorbiaceae	Tree
Kalanchoe integra	Crassulaceae	Herb
Tetrastragona eberhardtii	Vitaceae	Climber
Unknown	Unknown	Shrub
Chirita hamosa	Gesneriaceae	Herb
Stephania rotunda	Menispermaceae	Climber
Cymbidium sp.	Orchidaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Impatiens verrucifer	Basellaceae	Herb
Caryota baconensis	Palmae	Tree
Desmos cochinchinensis	Annonaceae	Climber
Laportea interrupta	Urticaceae	Herb

Table 12, continued

Laportea interrupta	Urticaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Wrightia macrocarpa	Apocynaceae	Tree
Ampelopsis cantoniensis	Vitaceae	Climber
Broussonetra papyrifera	Moraceae	Tree
Allophyllus sp	Sapindaceae	Shrub
Ageratum conzyoides	Compositae	Herb
Laportea interrupta	Urticaceae	Shrub
Laportea interrupta	Urticaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Unknown	Euphorbiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Mallotus philippinensis	Euphorbiaceae	Tree
Bauhinia ornata	Leguminosae-Caesalpinioideae	Climber
Cayratia wrayi	Vitaceae	Climber
Alchornia tiliaefolia	Euphorbiaceae	Tree
Kalanchoe integra	Crassulaceae	Herb
Tetrastragona eberhardtii	Vitaceae	Climber
Unknown	Unknown	Shrub
Chirita hamosa	Gesneriaceae	Herb
Stephania rotunda	Menispermaceae	Climber
Cymbidium sp.	Orchidaceae	Herb
Alangium kurzii	Alangiaceae	Tree
Impatiens verrucifer	Basellaceae	Herb
Caryota baconensis	Palmae	Tree
Alpinia tonkinensis	Zingiberaceae	Herb
Centotheca lappacea	Gramineae	Herb
Imperata cylindrica	Graminea	Grass
Bambusa sp	Gramineae-Bambusoideae	Tree
Bambusa sp	Gramineae	Tree
Sapium discolor	Euphorbiaceae	Tree

Table 12, continued

Paraboea swinhoii	Gesneriaceae	Herb
Laportea interrupta	Urticaceae	Herb
Laportea interrupta	Urticaceae	Herb
Laportea interrupta	Urticaceae	Herb
Quisqualis indica	Combretaceae	Climber
Zanthoxylum scabrum	Rutaceae	Shrub
Premna stenobotrys	Verbenaceae	Climber
Fagraea ceilanica	Loganiaceae	Climber
Vitis pentagona	Vitaceae	Climber
Iodes vitiginea	Icacinaceae	Climber
Amorphophalus tonkinensis	Araceae	Herb
Jasminum longisepalum	Oleaceae	Climber
Premna serratifolia	Verbenaceae	Climber
Claoxylon indicum	Euphorbiaceae	Tree
Laportea interrupta	Urticaceae	Herb
Impatiens verrucifer	Basellaceae	Herb
Alchornia tiliaefolia	Euphorbiaceae	Tree
Macaranga denticulate	Euphorbiaceae	Tree
Gnetum montanum.	Gnetaceae	Climber
Tridynamia eberhardtii	Convolvulaceae	Climber
Pachygone sp.	Unknown	Herb
Ficus pumila	Moraceae	Shrub
Lantana camara	Verbenaceae	Herb
Sygyzium sp.	Myrtaceae	Tree
Phyllanthus sp.	Euphorbiaceae	Shrub
Unknown	Orchidaceae	Herb
Croton sp	Euphorbiaceae	Shrub
Ficus microcarpa	Moraceae	Tree

Table 13: Third vegetation transect

Species	Family	Vegetation Type
Ageratum conzyoides	Compositae	Herb
Desmos cochinchinensis	Annonaceae	Climber
Alangium kurzii	Alangiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Alchornia tiliaefolia	Euphorbiaceae	Tree
Iodes vitiginea	Icacinaceae	Climber
Lantana camara	Verbenaceae	Herb
Broussonetra papyrifera	Moraceae	Tree
Sterculia lanceolata	Sterculiaceae	Tree
Amorphophalus tonkinensis	Araceae	Herb
Allophylus sp.	Sapindaceae	Shrub
Rhus chinensis	Anacardiaceae	Tree
Mallotus philippinensis	Euphorbiaceae	Tree
Desmos cochinchinensis	Annonaceae	Climber
Schefflera pes-avis	Araliaceae	Shrub
Maesa perlarius	Myrsinaceae	Shrub
Lygodium conforme	Schizeaceae	Climber
Vitis pentagona	Vitaceae	Climber
Smilax perfoliata	Smilacaceae	Climber
Camellia sp	Theaceae	Tree
Raphidophora decursiva	Araceae	Climber
Alangium kurzii	Alangiaceae	Tree
Tinospora sinensis	Menispermaceae	Climber
Maclura cochinchinensis	Moraceae	Climber
Psychotria sp	Rubiaceae	Climber
Paederia foetida	Rubiaceae	Climber
Alyxia sp.	Apocynaceae	Climber
Premna balansae	Verbenaceae	Climber
Dracaena cambodiana	Dracaenaceae	Tree
Pothos repens	Araceae	Climber
Phyllanthus sp	Euphorbiaceae	Shrub
Ficus sp	Moraceae	Tree
Stephania longa	Menispermaceae	Climber

Table 13, continued

Pteris multifida	Vittaroideae	Herb
Grewia asiatica	Tiliaceae	Tree
Litsea glutinosa	Lauraceae	Tree
Leea rubra	Leeaceae	Shrub
Zizyphus oenoplia	Rhamnaceae	Shrub
Merremia bimbim	Convolvulaceae	Climber
Cymbidium sp.	Orchidaceae	Herb
Ficus pumila	Moraceae	Tree
Ficus hispida	Moraceae	Tree
Zanthoxylum avicennae	Rutaceae	Shrub
Callicarpa girardiana	Verbenaceae	Shrub
Rubus alceaefolius	Rosaceae	Climber
Alangium kurzii	Alangiaceae	Tree
Rubus cochinchinensis	Rosaceae	Herb
Vigna sp.	Leguminosae-Papilionoideae	Herb
Clerodendrum cyrtophyllum	Verbenaceae	Shrub
Jasminum longisepalum	Oleaceae	Climber
Melastoma septemnervium	Melastomataceae	Shrub
Caryota baconensis	Palmae	Tree
Psidium guiava	Myrtaceae	Shrub
Celastrus sp	Celastraceae	Climber
Clerodendrum japonicum	Verbenaceae	Tree
Randia spinosa	Rubiaceae	Shrub
Saraca dives	Leguminosae-Caesalpinioidea	Tree
Celastrus sp	Celastraceae	Climber
Euodia lepta	Rutaceae	Tree
Phragmites vallatoria	Gramineae	Grass
Panicum curviflorum	Gramineae	Grass

Table 14: Fourth vegetation transect

Species	Family	Vegetation Type
Alangium kurzii	Alangiaceae	Tree
Alangium kurzii	Alangiaceae	Tree
Cayratia oligocarpa	Vitaceae	Climber
Ficus pumila	Moraceae	Tree
Streblus ilicifolia	Moraceae	Tree
Uvaria microcarpa	Annonaceae	Climber
Desmos cochinchinensis	Annonaceae	Climber
Adiantum soboliferum	Adiantaceae	Shrub
Lygodium conforme	Schizeaceae	Climber
Sinarundinaria sp.	Unknown	Tree
Semecarpus tonkinensis	Anacardiaceae	Tree
Alchornia tiliaefolia	Euphorbiaceae	Tree
Cipadessa baccifera	Meliaceae	Tree
Smilax sp.	Smilacaceae	Climber
Alangium kurzii	Alangiaceae	Tree
Pilea peltata	Urticaceae	Herb
Clerodendrum cyrtophyllum	Verbenaceae	Shrub
Phragmites vallatoria	Gramineae	Grass
Desmos cochinchinensis	Annonaceae	Climber
Alpinia tonkinensis	Zingiberaceae	Herb
Ventilago sp.	Rhamnaceae	Climber
Clematis granulata	Ranunculaceae	Climber
Alangium kurzii	Alangiaceae	Tree
Zanthoxylum nitidum	Rutaceae	Shrub
Ageratum conzyoides	Compositae	Herb
Pteris multifida	Vittaroideae	Herb
Pothos repens	Araceae	Climber
Pteris sp	Vittaroideae	Herb
Zanthocylum avicannae	Rutaceae	Shrub
Schefflera pes-avis	Araliaceae	Shrub
Impatiens verrucifer	Basellaceae	Herb
Impatiens verrucifer	Basellaceae	Herb

Table 14, continued

Celastrus sp	Celastraceae	Climber
Iodes vitiginea	Icacinaceae	Climber
Chirita drakei	Gesneriaceae	Shrub
Paraboea swinhoii	Gesneriaceae	Herb
Gnetum montanum	Gnetaceae	Climber
Bambusa sp.	Gramineae-Bambusoideae	Tree
Ficus sp	Moraceae	Tree
Stephania rotunda	Menispermaceae	Climber
Dracena cambodiana	Dracaenaceae	Tree
Hoya villosa	Asclepiadaceae	Climber
Pyrrosia lanceolata	Polypodiaceae	Herb
Bridelia sp.	Euphorbiaceae	Tree
Alocasia sp.	Araceae	Herb
Ficus benjamina	Moraceae	Tree
Alangium kurzii	Alangiaceae	Tree
Cymbidium sp.	Orchidaceae	Herb
Anthrophyum callifolium	Unknown	Shrub
Paederia foetida	Rubiaceae	Climber
Pandanus nanofratex	Pandanaceae	Shrub
Vitex trifolia	Verbenaceae	Shrub
Bauhinia ornate	Leguminosae-Caesalpinioideae	Climber
Unknown	Orchidaceae	Herb
Chirota hamosa	Gesneriaceae	Herb
Cycas sp	Unknown	Shrub

4.2 Phenology

4.2.1 Phenology Transects

Separate from the four vegetation transects which were used to identify the plant species on Dong Quyen Mountain, we established two phenology transects to monitor temporal plant part availability. The two phenology transects were established on Dong Quyen Mountain at the start of the study period in June 2007. For both transects, each plant within two meters of the transect line was given an aluminum tag. Diameter at breast height (DBH) was recorded for each plant (except climbers) and the plants were scored as climbers, herbs, shrubs, or trees. Species and family of all plants were recorded. Transects were monitored bimonthly. We recorded the presence or absence of young and mature leaves, flowers, and ripe and unripe fruit.

Transect One was 230 meters, covering an elevation of 92 meters. The total abundance of Transect One was 87 plants of 12 families comprised of 35 trees, 40 shrubs, 8 climbers, and 4 herbs. Species richness of Transect One was 19, 11 of which were shared with Transect Two. Nineteen plants had a DBH between 0-1.5 cm; 42 plants had a DBH between 1.5-3 cm; 9 plants had a DBH between 3-4.5 cm; 5 plants had a DBH between 4.5-6 cm; 3 plants had a DBH between 6-7.5 cm. Transect One had only one plant with a DBH greater than 10 cm (Table 15). The dominant species in Transect One were *Alchornia tilaefolia* (12 individuals), *Alangium kurzii* (11 individuals), and *Wrightia macrocarpa* (7 individuals). Transect One was located in the home range of the Valley Group.

Table 15: Phenology transect one

Tag Number	Species	Family	Type	DBH
100	*Alangium kurzii*	Alangiaceae	Tree	7.006
101	*Gnetum montanum*	Gnetaceae	Climber	Climber
102	Unknown		Shrub	1.273
103	*Derris tonkinensis*	Leguminosae-Papilionoideae	Climber	Climber
104	Unknown		Climber	Climber
105	*Sapium discolor*	Euphorbiaceae	Tree	2.388
106	*Alangium kurzii*	Alangiaceae	Tree	4.617
107	*Alangium kurzii*	Alangiaceae	Tree	1.751
108	Unknown (102)		Shrub	2.229
109	Unknown (102)		Shrub	1.592
110	*Wrightia macrocarpa*	Apocynaceae	Tree	1.592
111	Unknown (102)		Shrub	1.273
112	Unknown (102)		Shrub	1.592
113	*Eupatorium chinense*	Asteraceae	Herb	1.91
114	Unknown (102)		Shrub	1.433
115	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.433
116	Unknown (102)		Shrub	1.273
117	*Dracena cochinchinensis*	Dracenaceae	Tree	6.687
118	Unknown (102)		Shrub	1.751
119	Unknown (102)		Shrub	1.273
120	*Wrightia macrocarpa*	Apocynaceae	Tree	6.369
121	*Wrightia macrocarpa*	Apocynaceae	Tree	3.821
122	*Wrightia macrocarpa*	Apocynaceae	Tree	3.343
123	*Wrightia macrocarpa*	Apocynaceae	Tree	1.91
124	Unknown (102)		Shrub	1.751
125	*Ficus sp.*	Moraceae	Tree	10.031
126	*Wrightia macrocarpa*	Apocynaceae	Tree	1.91
127	Unknown	Euphorbiaceae	Shrub	1.273
128	*Premna balansae*	Verbenaceae	climber	1.433
129	Unknown (102)		Shrub	1.91
130	*Alangium kurzii*	Alangiaceae	Tree	5.254
131	Unknown (102)		Shrub	1.91

Table 15, continued

132	*Schefflera pes-avis*	Araliaceae	Tree	5.573
133	Unknown (102)		Shrub	2.07
134	Unknown	Euphorbiaceae	Tree	2.229
136	*Premna balansae*	Verbenaceae	climber	1.592
137	Unknown (102)		Shrub	1.433
138	*Wrightia macrocarpa*	Apocynaceae	Tree	3.662
139	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.751
140	Unknown		Climber	Climber
141	*Alangium kurzii*	Alangiaceae	Tree	3.821
142	*Mallotus philippinensis*	Euphorbiaceae	Tree	1.592
143	*Mallotus philippinensis*	Euphorbiaceae	Tree	1.273
144	Unknown (102)		Shrub	1.273
145	Unknown (102)		Shrub	1.273
146	Unknown (102)		Shrub	2.229
147	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.592
148	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	2.229
149	Unknown (102)		Shrub	2.388
150	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.91
151	Unknown		Tree	4.777
152	*Alangium kurzii*	Alangiaceae	Tree	4.14
153	*Alangium kurzii*	Alangiaceae	Tree	3.821
154	*Desmos chinensis*	Annonaceae	Shrub	1.592
155	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	2.547
156	Unknown		Tree	2.07
157	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.592
158	Unknown		Tree	1.433
159	Unknown		Tree	1.592
161	Unknown	Euphorbiaceae	Tree	1.433
162	Unknown	Annonaceae	Climber	Climber
163	*Litsea glutinosa*	Lauraceae	Tree	2.07
164	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.433
165	*Lantana camara*	Verbenaceae	Herb	1.592
166	Unknown (102)		Shrub	1.592
167	*Alangium kurzii*	Alangiaceae	Tree	4.458
169	*Alangium kurzii*	Alangiaceae	Tree	3.503
170	Unknown		Tree	1.91

Table 15, continued

171	Unknown	Euphorbiaceae	Climber	Climber
172	*Alangium kurzii*	Alangiaceae	Tree	4.458
173	Unknown (102)		Shrub	3.184
174	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	2.229
175	*Alangium kurzii*	Alangiaceae	Tree	5.095
176	*Desmos chinensis*	Annonaceae	Shrub	2.229
177	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	2.229
178	Unknown		Tree	1.592
179	*Eupatorium odoratum*	Asteraceae	Herb	1.592
180	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.273
181	Unknown	Euphorbiaceae	Shrub	1.91
182	Unknown	Euphorbiaceae	Tree	3.503
183	*Lantana camara*	Verbenaceae	Herb	2.229
184	*Alchornia tiliaefolia*	Euphorbiaceae	Shrub	1.273
185	*Desmos chinensis*	Annonaceae	Shrub	2.866
186	Unknown	Verbenaceae	Shrub	2.866
187	Unknown	Euphorbiaceae	Shrub	0.955
188	*Phyllanthus reticulates*	Euphorbiaceae	Shrub	1.592
189	*Streblus sp.*	Moraceae	Tree	1.91

Transect Two was 361 meters covering an elevation of 124 meters. Total abundance on Transect Two was 100 plants of 17 families comprised of 63 trees, 19 shrubs, 17 climbers, and 1 herb. Species richness on Transect Two was 21 species. Thirteen plants had a DBH between 0-1.5 cm; 46 plants had a DBH between 1.5-3 cm; 7 plants had a DBH between 3-4.5 cm; 10 plants had a DBH between 4.5-6 cm; 2 plants had a DBH between 6-7.5 cm; 1 plant had a DBH between 7.5-9 cm; 4 plants had a DBH that was greater than 10 cm (Table 16). The dominant species in Transect Two were *Wrightia* *macrocarpa* (19 individuals) and *Alangium kurzii* (10 individuals). Transect Two was located in the home range of the St6 group.

Table 16: Phenology transect two

Tag Number	Species	Family	Type	DBH
900	*Bambusa sp.*	Gramineae-Bambusoideae	Tree	5.095
899	*Ficus sp.*	Moraceae	Tree	16.879
898	*Sterculia sp.*	Sterculiaceae	Tree	15.764
897	*Sterculia sp.*	Sterculiaceae	Tree	17.993
896	*Sterculia sp.*	Sterculiaceae	Tree	10.509
895	*Streblus sp.*	Moraceae	Tree	4.140
894	*Dracena cochinchinensis*	Dracaenaceae	Tree	5.254
893	Unknown	Euphorbiaceae	Shrub	1.592
892	*Acalypha siamensis*	Euphorbiaceae	Herb	1.592
891	*Dracena cochinchinensis*	Dracenaceae	Tree	4.617
890	*Alangium kurzii*	Alangiaceae	Tree	2.388
889	*Taxillus chinensis*	Loranthaceae	Climber	Climber
888	*Ampelopsis heterophylla*	Vitaceae	Climber	Climber
887	*Premna balansae*	Verbenaceae	Climber	1.592
886	Unknown	Euphorbiaceae	Shrub	1.433
885	Unknown	Euphorbiaceae	Shrub	1.114
884	*Alangium kurzii*	Alangiaceae	Tree	1.433
883	*Mallotus philippinensis*	Euphorbiaceae	Tree	1.114
882	Unknown		Shrub	2.070
881	Unknown	Euphorbiaceae	Shrub	1.273
880	unknown (882)		Shrub	1.751
879	*Dracena cochinchinensis*	Dracenaceae	Tree	5.732
878	Unknown (882)		Shrub	1.433
877	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910
876	*Diospyros mollis*	Ebenaceae	Tree	1.751
875	*Diospyros mollis*	Ebenaceae	Tree	6.050
874	Unknown		Tree	2.388
873	Unknown (874)		Tree	1.433

Table 16, continued

872	*Bauhinia ornate*	Leguminosae-Caesalpinoidea	Climber	Climber
871	*Ficus sp.*	Moraceae	Tree	1.592
870	Unknown (874)		Tree	1.592
869	*Dracena cochinchinensis*	Dracenaceae	Tree	5.732
868	Unknown	Rubraceae	Tree	4.777
867	Unknown (874)		Tree	0.955
866	Unknown (874)		Tree	1.592
865	Unknown (874)		Tree	2.388
864	Unknown (874)		Tree	1.592
863	*Bauhinia ornate*	Leguminosae-Caesalpinoidea	Climber	Climber
862	*Desmos chinensis*	Annonaceae	Shrub	1.910
861	*Diospyros mollis*	Ebenaceae	Tree	2.547
860	*Alangium kurzii*	Alangiaceae	Tree	4.936
859	*Diospyros mollis*	Ebenaceae	Tree	4.617
858	*Mallotus philippinensis*	Euphorbiaceae	Tree	1.910
857	Unknown		Tree	3.821
856	*Wrightia macrocarpa*	Apocynaceae	Tree	2.229
855	*Mischocarpus pentapetalus*	Sapindaceae	Tree	7.643
854	*Dracena cochinchinensis*	Dracenaceae	Tree	5.732
853	Unknown		Shrub	1.433
852	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910
851	Unknown (853)		Shrub	1.751
850	*Wrightia macrocarpa*	Apocynaceae	Tree	2.547
849	*Wrightia macrocarpa*	Apocynaceae	Tree	2.229
848	*Ioides cirrhosa*	Icacinaceae	Climber	Climber
847	*Wrightia macrocarpa*	Apocynaceae	Tree	2.229
846	*Zanthoxylum laetum*	Rutaceae	Climber	Climber
845	*Hiptage candicans*	Malpighiaceae	Climber	Climber
844	*Ficus microcarpa*	Moraceae	Tree	6.687
843	*Zanthoxylum laetum*	Rutaceae	Climber	Climber
842	*Mallotus philippinensis*	Euphorbiaceae	Tree	0

Table 16, continued

841	Unknown	Rubraceae	Shrub	1.592
840	*Alangium kurzii*	Alangiaceae	Tree	1.751
839	*Zanthoxylum laetum*	Rutaceae	Climber	Climber
838	*Desmos chinensis*	Annonaceae	Shrub	1.592
837	*Zanthoxylum laetum*	Rutaceae	Climber	Climber
836	*Bauhinia rubro-villosa*	Leguminosae-Caesalpinoidea	Climber	Climber
835	*Wrightia macrocarpa*	Apocynaceae	Tree	3.821
834	*Premna balansae*	Verbenaceae	Climber	1.751
833	*Alangium kurzii*	Alangiaceae	Tree	1.910
832	Unknown	Apocynaceae	Climber	Climber
831	*Wrightia macrocarpa*	Apocynaceae	Tree	1.751
830	*Prunus fordiana*	Rosaceae	Tree	3.503
829	Unknown	Euphorbiaceae	Tree	2.547
828	*Wrightia macrocarpa*	Apocynaceae	Tree	4.299
827	*Alangium kurzii*	Alangiaceae	Tree	3.184
826	*Alangium kurzii*	Alangiaceae	Tree	5.573
825	*Dracena cochinchinensis*	Dracenaceae	Tree	5.095
824	*Wrightia macrocarpa*	Apocynaceae	Tree	1.751
823	*Alangium kurzii*	Alangiaceae	Tree	2.547
822	*Wrightia macrocarpa*	Apocynaceae	Tree	2.547
821	*Alangium kurzii*	Alangiaceae	Tree	1.592
820	*Gnetum latifolium*	Gnetaceae	Climber	Climber
819	Unknown		Shrub	1.592
818	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910
817	*Bauhinia ornate*	Leguminosae-Caesalpinoidea	Climber	Climber
816	Unknown		Shrub	1.751
815	Unknown (816)		Shrub	1.592
814	*Premna balansae*	Verbenaceae	Climber	1.114
813	Unknown (816)		Shrub	1.273
812	*Wrightia macrocarpa*	Apocynaceae	Tree	3.184
811	Unknown		Shrub	1.592
810	*Wrightia macrocarpa*	Apocynaceae	Tree	2.388
809	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910

Table 16, continued

808	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910
807	Unknown		Shrub	1.433
806	*Wrightia macrocarpa*	Apocynaceae	Tree	1.910
805	*Alangium kurzii*	Alangiaceae	Tree	1.273
804	*Wrightia macrocarpa*	Apocynaceae	Tree	2.547
803	*Schefflera pes-avis*	Araliaceae	Tree	2.707
802	*Debregeasia squamata*	Urticaceae	Shrub	1.592
801	*Wrightia macrocarpa*	Apocynaceae	Tree	2.070

4.2.2 Plant Part Abundance and Consumption

Plant parts showed seasonal abundance (Figure 4). Young and mature leaves were the most abundant parts throughout the year. The lean months were December-February, when mean temperatures and young leaf abundance were the lowest. The abundance of all plant parts was lowest during this time, and many deciduous trees lost their leaves completely. Nearly 100% of plants had young and mature leaves in the wet season of May-October with a decrease of both recorded in November. After decreased leaf production in the winter months, young leaves started to increase in March while mature leaves were observed in increasing abundance in April. Flowers were most abundant during May through October with peak abundance in October. Fruit was generally most abundant in July-October with almost no ripe or unripe fruit during January, February, and March. Along with flowers, peak fruit abundance was October 2007.

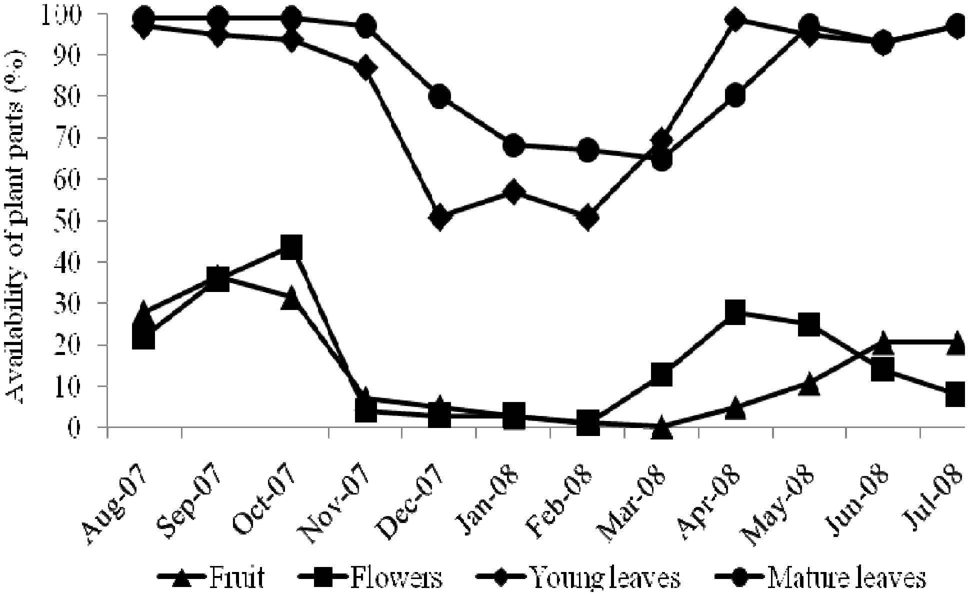

Figure 4: Phenological changes in the abundance of plant parts from August 2007-July 2008

The temporal consumption of different plant parts was not tied to the abundance of those plant parts in the habitat over the 11 month period. Across months, there were no significantly positive relationships between the consumption and abundance of young leaves (r_s=0.188, P=0.57, N=11), mature leaves (r_s=0.445, P=0.17, N=11), fruit (r_s=0.370, P=0.26, N=11), or flowers (r_s=0.305, P=0.36, N=11) (Figures 5, 6, 7, and 8). Despite the lack of significance in these relationships, however, there are interesting patterns in the abundance and consumption of plant parts over the months. Young leaf abundance was lowest during December and February. As leaf bud and young leaf availability rose in March and April, langur consumption similarly rose. Availability and consumption of young leaves then diverged in the summer months, a time when unripe fruit consumption rose. Mature leaf consumption showed a small spike in February, corresponding to a time when young leaf availability was lowest. Mature leaves contributed their smallest amount to the langur diet during March-May when young leaf availability was peaking.

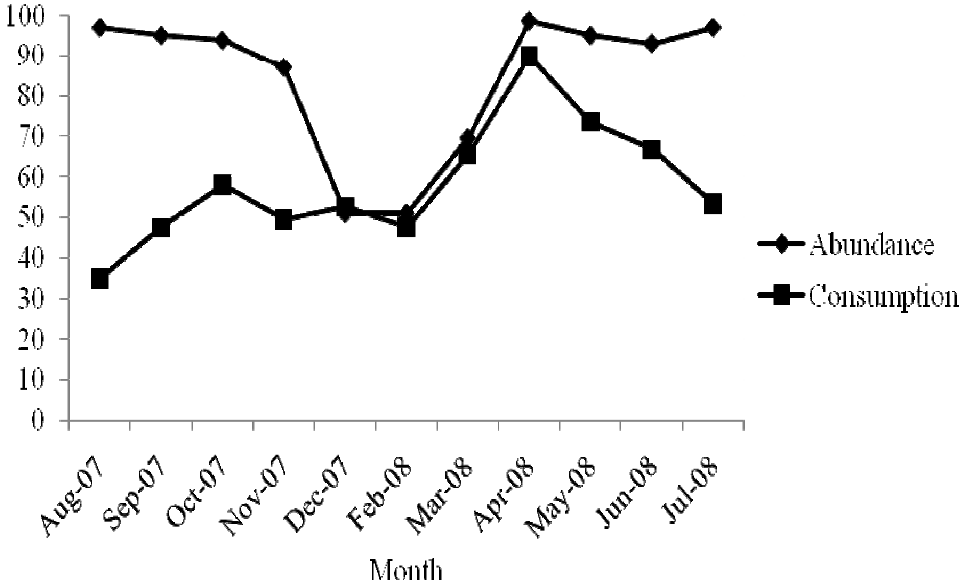

Figure 5: Monthly abundance and consumption of young leaves

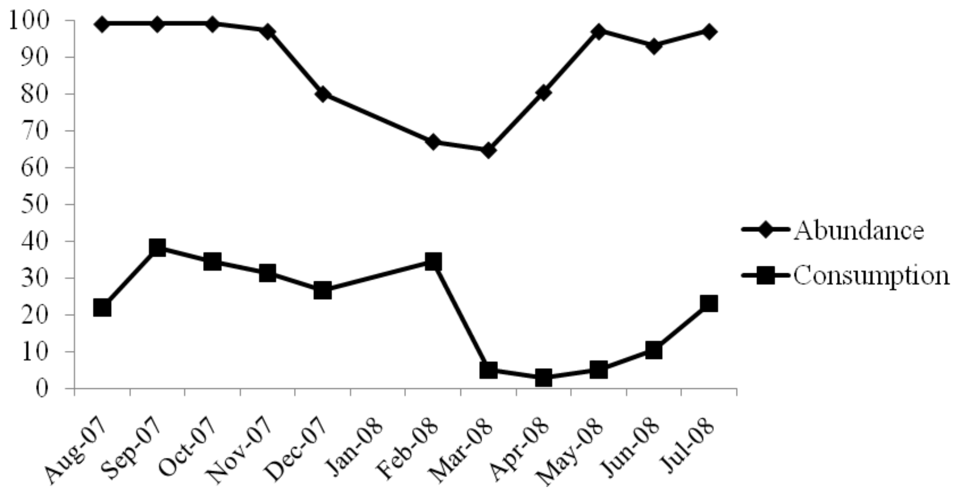

Figure 6: Monthly abundance and consumption of mature leaves

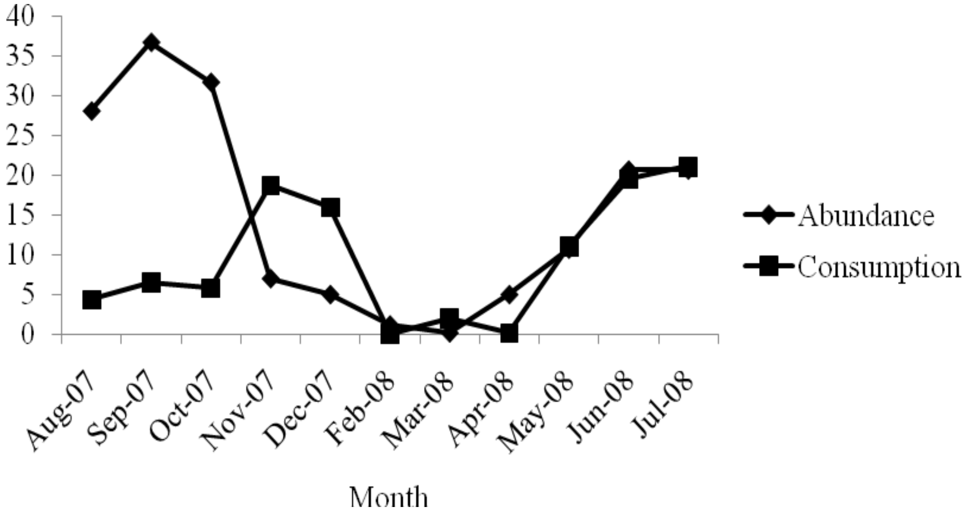

Figure 7: Monthly abundance and consumption of unripe fruit

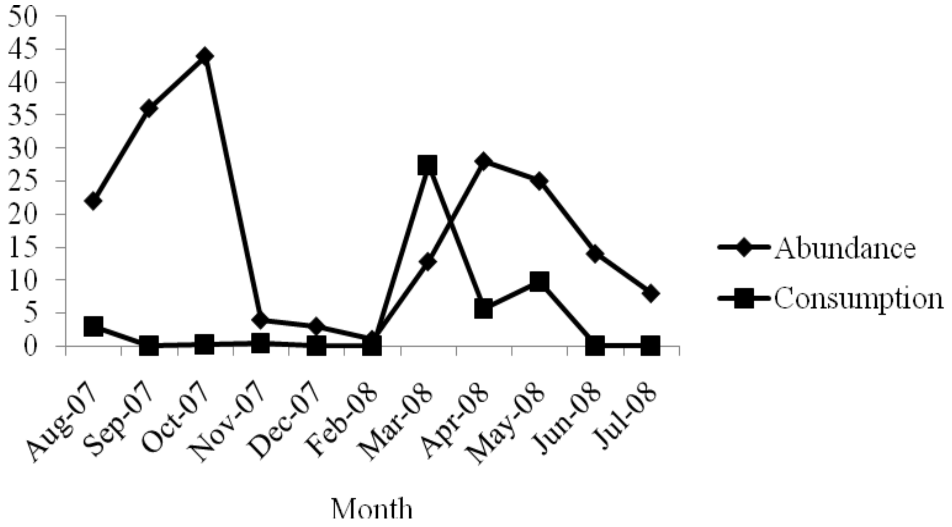

Figure 8: Monthly abundance and consumption of flowers

4.3 Weather

The mean daily temperature from July 2007 through July 2008 was 22.9 º C. During the study period, the total rainfall was 1591.92 mm (July 2007-July 2008) (Figure 9). Total annual rainfall over a twelve month consecutive period (August 2007-July 2008) was 1375.62 mm. The driest months were November and December and the wettest month was October, when a typhoon came through, flooding much of Van Long and the surrounding communities. After October, June and July were the months with the most rainfall. Monthly maximum temperatures varied from18.8 º C in February 2008 to 36.9 º C in June 2008 while monthly minimum temperatures varied from 8.8 º C in February 2008 to 27.6 º C in June 2008. Average monthly temperatures ranged from a low of 12.9 º C in February 2008 to a high of 30.6 º C in July 2008 (Figure 9). Monthly maximum humidity levels varied from 82 in November 2007 and May 2008 to 91 in July 2008 while monthly minimum humidity levels varied from 39 in November 2007 to 70 in December 2007. Average monthly humidity levels ranged from a low of 67.7% in November 2007 to a high of 80.8% C in December 2007. Only in the month of November was the average humidity level less than 70% (Figure 10).

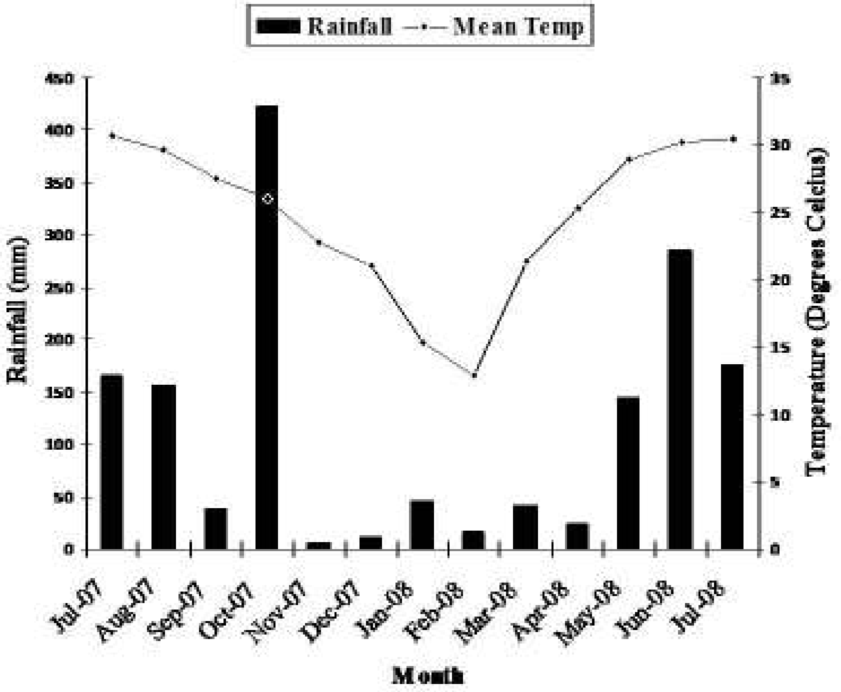

Figure 9: Monthly rainfall and mean temperature, July 2007-July 2008

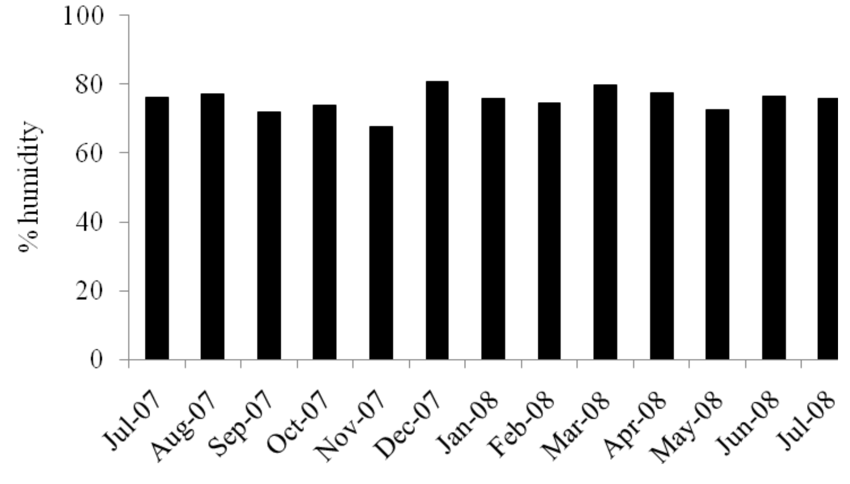

Figure 10: Monthly mean humidity, July 2007-July 2008

5. Diet and Feeding Ecology

5.1 Introduction

An accumulation of ecological research on the Colobinae of Africa and Asia has revealed them to be broader than a group of simple arboreal leaf-eaters. In addition to dietary flexibility, colobines inhabit diverse climatic and environmental conditions, from the dry season of northern India where langurs go for months without drinking water (Jay, 1965), to the 4,200 meter-high conifer forest mountains of Tibet and China (Xiao et al., 2003). Further expanding the boundaries of colobine adaptive diversity are the ecologically descriptively-named 'limestone langurs' of Southeast Asia, six taxa restricted to limestone karst habitat. Karst refers to areas where carbonate rocks, mostly limestone, are exposed (LeGrand, 1973). Many plants cannot grow on limestone soils, due either to the high alkalinity, toxic levels of calcium, or limited availability of iron and manganese (McAleese and Rankin, 2003), and vegetation on karst is notoriously stunted and rich in endemic plants (Urich, 1989; Huang et al., 2000; Li et al., 2003; Day and Chenoweth, 2004; Liu et al., 2004). Limestone karst is a distinct habitat, and therefore characterizing the diet of langurs inhabiting limestone forests is important to understanding the total range of colobine dietary diversity. A central question in the study of limestone langurs is whether the current restriction of these langurs to limestone karst is as refuge habitat or is based on ecological dependencies (Li and Rogers, 2005). Several hypotheses have been offered to explain the distribution of langurs on limestone karst habitat, and in this paper I offer a preliminary test of one of these hypotheses, i.e. that dealing with feeding ecology.

The limestone langurs of the genus *Trachypithecus* include six allopatric taxa, *T. poliocephalus leucocephalus* (endemic to China), *T. francoisi* (of Vietnam and China), *T. delacouri* and *T. poliocephalus* (endemic to Vietnam), *T. laotum* (endemic to Laos), and *T.l. hatinhensis* (of Laos and Vietnam). Researchers have studied the diet and feeding behavior of *T. p. leucocephalus* and *T. francoisi* in China (Huang et al., 2000; Li et al., 2003; Li and Rogers, 2006; Zhou et al., 2009a) yet systematic studies on the feeding ecology of the four other taxa in this monophyletic group have not yet been conducted. With only about 200 individuals remaining in 50-57 groups in 18 isolated subpopulations, Delacour's langurs are listed as Critically Endangered (Nadler et al., 2008). Populations occur in four provinces in northern Vietnam, comprising an area of 5,000 square kilometers, of which actual locales comprise 400 square kilometers (Nadler, 2004; Tilo Nadler, personal communication). Due to small and isolated subpopulations, high historic hunting pressure, and the difficulty of working on rugged limestone topography, Delacour's langurs are not well habituated to observers and cannot be studied for long periods of time. All dietary information on this species has come from anecdotal observations and from captive studies (Klein, 1999; Tran Thi Thao, 2001; Le Van Dung, 2007).

In this study I present data on the diet and feeding behavior of Delacour's langurs on Dong Quyen Mountain in Van Long Nature Reserve from August 2007 through July 2008. The main objective of this study was to characterize the diet of Delacour's langurs during the study period and then use these data to evaluate the hypothesis of dependency on limestone endemic plant species. The study population was unhabituated and the topography of limestone karst made observations extremely difficult compared to other non-karstic colobine sites in Africa and Asia. The number of data hours is therefore comparatively small, yet this study is the most comprehensive to date on the diet of this critically endangered and little-known species.

5.2.1 Study Site

Research was conducted at the Dong Quyen karst mountain of Van Long Nature Reserve (20°20′55″N, 105°48′20″E) in Ninh Binh Province, northern Vietnam, about 80 km from Hanoi. Van Long Nature Reserve (VLNR) is a wetland with standing water surrounding the mountains where langurs live. In the southeastern part of the reserve, wet marshes fragment the mountain ranges into separate limestone island blocks. The primary study site is one such 265-hectare block, Dong Quyen, which rises from 1 m to 328 m elevation. This site was chosen because langurs are most easily seen here and Dong Quyen Mountain contains about 70 langurs, the largest subpopulation of Delacour's langurs in the world.

The dominant vegetation at VLNR is a mixture of mostly evergreen and some deciduous forest on limestone and arenaceous hills, of which the highest peak is 428 meters (Nguyen Ngoc Quynh, 2001). No plant species or family dominates the flora at VLNR. Vegetation on Dong Quyen Mountain is comprised of woody trees and shrubs (44%), herbs (25%), climbers (30%), and grasses (1%) and a total of 145 plant species, based on vegetation transects conducted in June-July 2006 (Workman and Nguyen The Cuong, unpublished data). From July 2007-July 2008, the mean monthly maximum temperature was 31°C, and the mean minimum was 13°C (N=394, range=9-37 °C). Relative humidity ranged from 39% to 91% with a mean of 75%. Total annual rainfall during the study period was 1375.62 mm, with 89% of rain falling between May-October. I recognized a wet and dry season based on this distribution.

5.2.2 Feeding Ecology of Delacour's Langurs

I collected data from August 2007-July 2008. Because Dong Quyen is surrounded throughout the year by water between 1-4 meters deep, I pushed a bamboo boat through the wetland each morning, scanning Dong Quyen and collecting data whenever I located a group of langurs. I knew the approximate location of groups from previous survey work. I observed seven groups for information on diet, but concentrated my searching and observation efforts on three groups that were most visible. When one of these three groups could not be found, I looked for another group. I collected data on adult males, adult females (some of whom had dependent young), and subadults. Focal animals were chosen randomly each day, based on which langur group was encountered. I was only able to confidently identify a few langurs as individuals, and therefore data collection focused on a rotation of age and sex class.

When I encountered a langur group, I used the instantaneous focal-animal sampling method (Altmann, 1974) to record all occurrences of behavior in the specified categories “rest,” “social,” “travel,” “drink,” and “feed” for as long as it was possible to follow the focal individual (N=372 hours; 203 days). Feeding was recorded as any occasion when a langur took or moved vegetation towards its mouth, ingested, masticated, or swallowed food (Fashing, 2001a). The focal-animal method maximized the amount of data that could be obtained from these elusive animals (Altmann, 1974). I used Canon 18x50IS binoculars and a Bushnell Trophy 20-60x65 spotting scope, from a distance of between 50-400 meters. VLNR’s topography is characterized by steep cliffs which caused langur groups to be frequently out of sight and which did not permit following the same group every day. However, the boat allowed quick responses to langur movements compared to slow and dangerous travel on the karst. In addition, langurs were not fully habituated at VLNR, but would tolerate closer approach (<10 meters) by humans in the boat. For these reasons, making observations from the boat was the best way to collect behavioral data. I realize, however, that the data presented here may not provide a complete dietary profile of this species because the habitat’s steep cliffs and the difficulty of following the animals throughout the habitat limited observations. Similar limitations also have been noted for other limestone langur studies (Li and Rogers, 2006).

Instantaneous feeding data were collected on focal individuals. When a focal animal was feeding, the species and plant part (young leaves, mature leaves, unripe fruit, ripe fruit, flowers, buds, stems, and seeds) consumed was noted. When an animal was feeding but the plant item could not clearly be seen, the item was classified as unidentified. I measured feeding effort rather than food intake and therefore all dietary data are expressed as a percentage of feeding records (Li and Rogers, 2006). Harrison et al. (2009) noted that feeding time is a commonly used method in primatology, although percentage of time spent feeding on major food types can be problematic since different species and individuals have different intake rates for different food types. Feeding records for each focal session were combined to calculate average proportion of feeding time to different foods and plant species for each month. Monthly feeding records were combined to determine an annual feeding record. Throughout the course of the project, unknown foods eaten by the Delacour’s langurs were identified by Nguyen The Cuong of the Institute for Ecology and Biological Resources and Nguyen Manh Cuong of Cuc Phuong National Park.

5.2.3 Statistical Analyses

The contributions of different food species and plant parts to the Delacour’s langurs’ annual feeding habits were calculated as a proportion of the total number of all feeding records (N=5,949; 108 hours). Monthly feeding habits were calculated as proportions of the feeding records for each month. Based on rainfall results over the study period, feeding differences were analyzed between a wet and dry season. August-October 2007 and May-July 2008 are used as the wet season and November- April 2008 the dry season. January 2008 was excluded from seasonality analyses, as very limited behavioral data exist for this month. This study complied with the Institutional Animal Care and Use Committee of Duke University, Durham, NC, with the ASP Principles for the Ethical Treatment of Non Human primates, and with Vietnamese law.

5.3 Results

5.3.1 Annual Dietary Composition: Plant Parts and Species

Delacour's langurs spent 29% of their activity budget feeding. The general plant types in the langurs' diet included trees and shrubs (45%), climbers (53%), and one herb species (2%). The plant diet of the langurs was principally composed of young leaves (58%) followed by mature leaves (20%), unripe fruits (9%), and flowers and flower buds (5%). Leaf buds, seeds, stems, and ripe fruit each composed less than 1% of the annual plant diet, and the remaining 5% of the plant diet consisted of unidentified items. Langurs were never observed eating any animal or invertebrate matter, although juvenile and subadult langurs were seen chasing squirrels on a few occasions. Langurs drank water, both from the wetland and from karst bowls.

Data on plant part consumed were available for 95% of the total feeding records. Leaves were eaten from all but four (*Lantana camara, Cocculus sarmentosus, Taxillus sp.,* and *Eriobotrya bengalensis*) of the 42 eaten species. From these four species, langurs ate only the unripe fruit. The majority of the fruit that the langurs consumed was that of *Lantana camara;* langurs ate only the fruit –and almost exclusively the unripe fruit- of this plant. *Lantana camara* is not a limestone endemic plant, but rather a weed native to tropical America which has wide ecological tolerances, permitting it to grow in a broad range of geographic and climatic conditions and to earn nomination among 100 of the "world's worst" invaders (Walton, 2006). Indeed, *Lantana camara* is found along roadsides and in cultivated gardens across the Old and New Worlds.

Table 17: Plants consumed by Delacour's langurs on Dong Quyen Mountain

Family	**Genera**	**Species**	**Family**	**Genera**	**Species**
Alangraceae	1	1	Malpighiaceae	1	1
Apocynaceae	1	1	Menispermaceae	3	3
Araceae	1	1	Moraceae	3	4
Caesalpinaceae	1	1	Oleaceae	1	1
Combretaceae	2	2	Rosaceae	2	2
Convolvulaceae	2	2	Rubiaceae	2	2
Dioscoreacea	1	1	Rutaceae	2	2
Ebenaceae	1	1	Sterculiaceae	1	1
Euphorbiaceae	5	6	Uderbenaceae	1	1
Fabaceae	1	1	Urticaceae	1	1
Flacourtiaceae	1	1	Verbenaceae	1	1
Loxanthaceae	1	1	Unidentified families	4	4

Data on species consumed were available for 67% of all feeding records (N=3,986). Langurs were observed feeding from a total of 42 species belonging to at least 36 genera and 24 families (Table 17). Sixteen plant species each contributed at least 1% of the annual feeding records, and these species together constituted at least 93% of the total feeding records (Table 18). The top four plant species- all native to eastern Asia but not endemic to limestone- comprised over half (56%) of the langurs' annual feeding records, and the ten most frequently-consumed species together made up at least 84% of the feeding records. The langurs fed most frequently on the young leaves, mature leaves, and flowers of *Broussonetia papyrifera* (22%), a native East Asian plant but one found in a variety of habitats and even considered invasive in areas where it has been introduced (Zheng et al., 2004). Langurs also fed frequently on the young and mature leaves of *Wrightia macrocarpa* (13%), the young leaves, mature leaves, and flowers of *Alangium kurzii* (11%), followed by the young leaves, mature leaves, and unripe fruit of *Ficus microcarpa* (9%). No other plant species contributed more than 8% to the total annual feeding records.

Table 18: Species contributing at least 1% of annual feeding records, ranked in order of percent contribution

	Family	Species	Parts Eaten[a]	Percent Annual Feeding Records	Months Consumed[b]	Plant Endemic to Limestone Karst[c]
1	Moraceae	*Broussonetia papyrifera*	yl, ml, fl	22	10	No
2	Apocynaceae	*Wrightia macrocarpa*	yl, ml, fl	13	9	No
3	Alangraceae	*Alangium kurzii*	yl, ml, fl, lb	11	9	No
4	Moraceae	*Ficus microcarpa*	yl, ml, uf, rf	9	9	No
5	Uderbenaceae	*Lantana camara*	Uf	7	6	No
6	Euphorbiaceae	*Alchornia tiliaefolia*	yl, ml	6	6	No
7	Fabaceae	*Derris tonkinensis*	yl, ml, fl, lb, se	5	7	No
8	Convolvulaceae	*Ipomoea bonii*	yl, ml, fl, lb, st	4	4	No
9	Oleaceae	*Linociera verticillata*	yl, ml, uf, lb	3	6	No
10	Ebenaceae	*Diospyros mollis*	yl, ml, uf	2	6	No
11	Rubiaceae	*Gardenia tonkinensis*	yl, ml, uf	2	3	No
12	Euphorbiaceae	*Mallotus philippensis*	yl, ml, uf	<2	7	No
13	Euphorbiaceae	*Bridelia retusa*	Yl	<2	2	No
14	Urticaceae	*Debregeasia squamata*	Yl	<2	2	No
15	Malpighiaceae	*Hiptage lucida*	Yl	1	1	No

Table 18, continued						
16	Menispermaceae	*Stephania rotunda*	yl, ml, uf	1	5	No

[a]yl=young leaf, ml=mature leaf, uf=unripe fruit, rf=ripe fruit, fl=flower, lb=leaf bud, st=stem, se=seed

[b]Out of a total of 11 months (January not included in annual diet)

[c]Sources: Soejarto et al., 2004; Nguyen Manh Cuong (personal communication)

5.3.2 Temporal Patterning of Feeding Behavior: Plant Parts and Species

Comparing the dry and wet seasons, langurs ate young leaves (63 vs. 56%), mature leaves (18 vs. 23%), fruit (9 vs. 10%), seeds (1.1 vs. 0%), and flowers (8 vs. 2%). Despite little variation between seasons, monthly variation is evident (Figure 11). Feeding on young leaves peaked at 90% in April, and reached its lowest at 35% in August. Young leaves accounted for at least 35% of feeding records in all 11 months of feeding analyses. While mature leaves were eaten in every month, the langurs' consumption of mature leaves varied extensively, peaking at 38% in September, but reaching a low of 3% in April, when young leaf consumption was highest. Although the top 16 plant species together comprised at least 93% of the langurs'annual feeding records, their inclusion was quite variable on a monthly basis. Clear seasonal patterns existed in the langurs' consumption of four of the top five consumed species: *Broussonetia papyrifera, Wrightia macrocarpa, Alangium kurzii,* and *Lantana camara,* but not of *Ficus microcarpa* (Figure 12). The langurs' consumption of *Alangium kurzii* displayed the greatest seasonal disparity, contributing 25% of the wet season feeding records, but only 5% during the dry season.

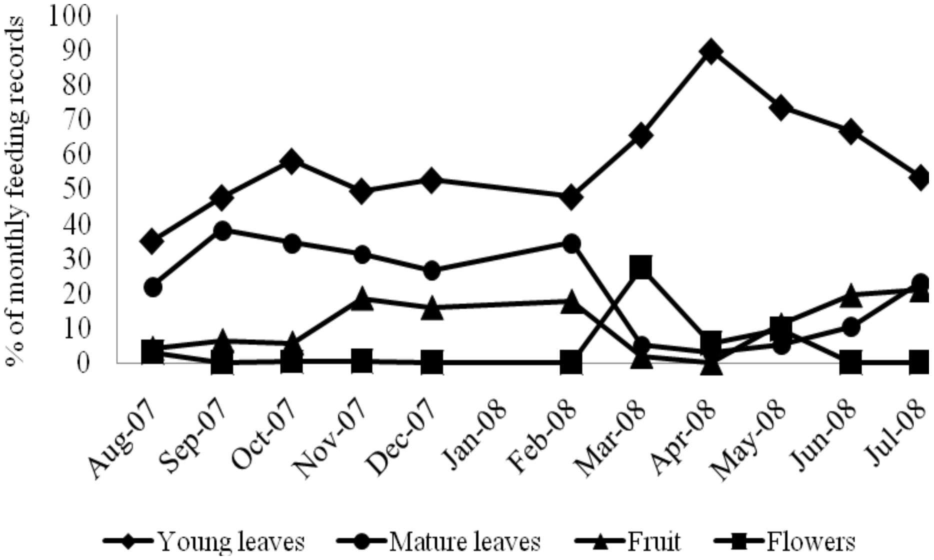

Figure 11: Monthly changes in the proportion of different plant parts in the diet of Delacour's langurs (August 2007-July 2008). August does not add up to 100% because 35% of the diet came from unidentified items

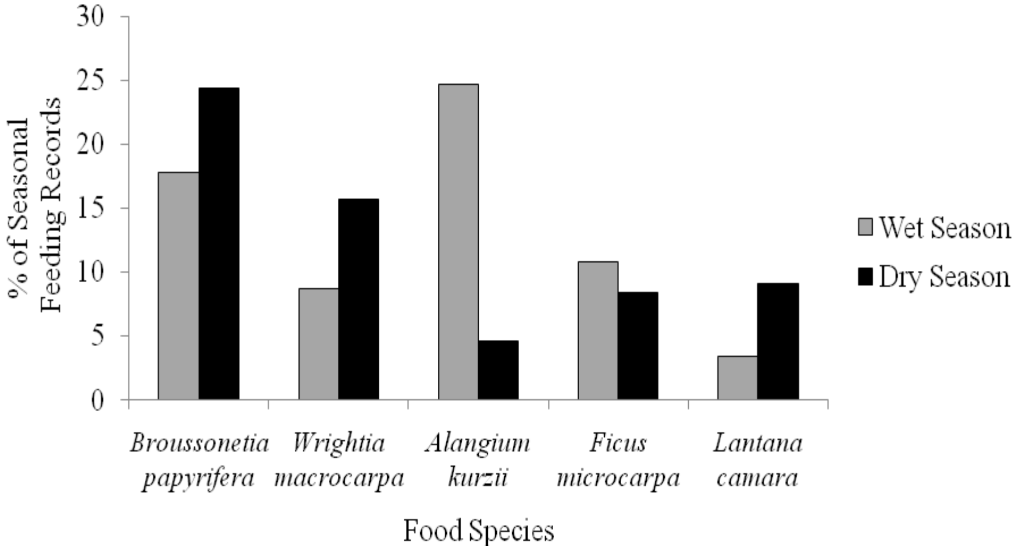

Figure 12: Seasonal consumption of Delacour's langurs' five most important species

5.4 Discussion

The most important plant species in the diet of *Trachypithecus delacouri* at VLNR during August 2007-July 2008 were not plants endemic to limestone habitats. During the study period, leaves comprised the overwhelming majority of the Delacour's langur diet and young leaves contributed the greatest propotion to the diet annually and across months and seasons. Mature leaf and fruit consumption rose only at times of the year when young leaf consumption declined. Delacour's langurs limited their feeding to 42 of 145 plant species. More than 93% of the Delacour's langurs' diet came from only 16 of plant species, none of which were limestone endemics.

5.4.1 Comparisons with Other Colobines

The limestone langurs *Trachypithecus poliocephalus leucocephalus and T. delacouri* are among the most folivorous of the Asian colobines (Table 19). In fact, when mature and young leaves are combined for comparison, both of the limestone langurs are more folivorous than any of the other Asian species for which data are known. Compared to the Yunnan snub-nosed monkey (*Rhinopithecus bieti*), another Asian langur found in mountain habitats, Delacour's langur- and limestone langur- diets are narrow and simple. *Rhinopithecus bieti* shows extreme lichen specialization (nearly 70% of feeding records) at the higher altitude parts of its range (Kirkpatrick, 1996), and extreme dietary diversification (fungi, squirrel meat, underground storage organisms, terrestrial herbaceous vegetation, and snow) at lower altitudes (Ding and Zhao, 2004; Grueter et al., 2009a). Delacour's langurs were never observed ingesting invertebrates, animal matter, or lichens.

Table 19: Dietary comparison (%) between Delacour's langurs and other colobines

Species	L	YL[a]	ML	FL	F/S	O	Source
Trachypithecus delacouri	80	60	20	5	9	6	this study
T. p. leucocephalus	83.3	74.9	8.4	2.4	7.7	2.2	Li et al., 2003
T. p.leucocephalus	89	75.2	10.5	2.7	6.1	2.2	Li & Rogers, 2006
T. auratus	56	46	<10	14	32	8	Kool, 1993
T. pileatus	53	11	42	7	34	1	Stanford, 1991
T. johnii	52	25	27	9	25	6	Oates et al., 1980
T. obscures	58	36	22	7	35		Curtin, 1980
T. vetulus	60	20	40	12	28		Hladik, 1977
Presbytis rubicund	37	36	1	11	49	2	Davies, 1984
P. siamensis	35	24	11	6	56	2	Curtin, 1980
P. hosei	78	45	5	3	19		Mitchell, 1994
Pygathrix nigripes	54.6			14.6	29.3	1.5	Duc et al., 2009
Nasalis larvatus	74	73	<1	8	11	8	Boonratana, 1994
N. larvatus	52	41	11	3	40	5	Yeager 1989
Rhinopithecus roxellana	24				29.4	41.4	Guo et al., 2007
R. bieti	34					69	Ding & Zhao, 2004
Colobus guereza	87.5	72.3	27.2	2.2	7.5	2.8	Harris & Chapman, 2007

L=Total leaves; YL=young leaves; ML=mature leaves; FL=flowers; F/S=fruit and/or seeds; O=other or unidentified items

[a] Young leaves includes leaf buds

In a recent review chapter, Kirkpatrick (2007) described Asian colobines as feeding predominantly on young leaves, supplementing with seeds and fruits. However, both Delacour's langurs and *Trachypithecus leucocephalus* include comparatively small proportions of seeds in their diet (<1%). At VLNR, seed consumption was absent from all months except February, when it accounted for 18% of feeding records. Further, the overall contribution of fruit to the diet of *T. delacouri* was dramatically low (less than 1/3 the amount) compared to other *Trachypithecus*' diets (Table 19). Li and Rogers (2006) suggested this might be due to a lack of suitable or seasonally available fruit in the limestone karst environment, and that langurs would eat more fruit if more fruit were available. While this study supports this contention for limestone karst environments, fruit abundance needs to be quantified to clarify whether karstic environments have lower fruit and seed productivity. During November and December, fruit of *Lantana camara* seemed to be most available in the habitat and accounted for the second-greatest proportion of the diet after *Broussonetia papyrifera*, suggesting a preference for this fruit when available.

Temporal variation in plant parts eaten by primates- including colobines- is large (Chapman et al., 2002), but limestone langurs show less drastic seasonal variation than other colobines. In southern China, *Trachypithecus poliocephalus leucocephalus* shows a preference for young leaves, even in winter (Li, 2000; Li et al., 2003). The Delacour's langurs' similar fidelity to young leaves seems to be made possible by the abundance of young leaves throughout the year. In all months, young leaves contributed the greatest percentage to the diet of Delacour's langurs at VLNR, never falling below 35% of feeding records. Asynchronous flushing of young leaves throughout the year provides consistent edible foliage and might contribute to high primate folivore biomass (Ripley, 1979). At VLNR, asynchronous flushing of preferred young leaves –along with cessation of hunting in 2001- may explain the quick rebound of the langur population on Dong Quyen Mountain. While Delacour's langurs supplemented their young leaf consumption with mature leaves, they were similar to other langurs in mostly excluding mature leaves, which were the most consistently available item in the habitat (Kool, 1993).

The mostly folivorous diet of Delacour's langurs- as well as of *T. p. leucocephalus*- may also be explained by the kinds of trees present on limestone karst. Dong Quyen Mountain is unlike many Southeast Asian forests because it is not dominated by Dipterocarps. In SE Asia, habitats that have an abundance of Dipterocarps typically have few leguminous trees, and vice versa (Waterman et al., 1988). Dong Quyen Mountain, however, has neither an abundance of Dipterocarpaceae nor Leguminoseae. No plant family or species dominates the flora at either VLNR or Fusui Nature Reserve, China (Li et al., 2003). Vegetation communities growing over limestone are distinct in species composition from other forest types (Sterling et al., 2006). In Kalimantan, forest-covered karsts have roughly one-third of the plant diversity present in lowland Dipterocarp forests (MacKinnon et al., 1996; Marshall et al., 2007). It may be that the absence of the dipterocarps' relatively indigestible foliage (Waterman et al., 1988) and the absence of exploitable leguminous seeds contribute to high folivory, especially of young leaves, by langurs living on limestone. While leaves eaten by Delacour's langurs during this study period contained significantly higher protein:fiber ratios than non-eaten leaves, eaten and non-eaten leaves did not differ in other tested chemical constituents; seeds were not analyzed for their phytochemical content (Workman and Le Van Dung, 2009; Chapter 6).

5.4.2 Does Reliance on Karstic Endemic Plants Explain Limestone Langur Distribution?

Five hypotheses have been offered to explain the utilization of karst habitat by limestone langurs: 1) retreat after loss of habitat; 2) reliance on endemic plants; 3) protection from predators by use of sleeping sites; 4) shelter against climatic conditions; 5) presence of water. So far there has been no support for the endemic plants hypothesis. In southern China, *Trachypithecus poliocephalus leucocephalus* eat a variety of plant species, show dietary flexibility, and show no reliance to plants that are endemic to limestone habitats (Huang et al., 2000; Li et al., 2003). At the Endangered Primate Rescue Center in northern Vietnam, *T. delacouri, T. laotum, T. laotum hatinhensis*, and *T. poliocephalus* eat the leaves, bark, flowers, and fruit from more than 100 species, but less than 10% of these are typical limestone species (Tilo Nadler, personal communication). Such dietary information, along with activity budget data from *T. p. leucocephalus* at different levels on limestone hills, led Li and Rogers (2005) to conclude that coevolution between limestone forests and langurs was unlikely. They explain the use of karsts habitats as a refuge rather than as an ecological dependency. While data have not championed a dietary explanation for the distribution of limestone langurs, data are still needed from several of the limestone langurs in their natural habitat to fully evaluate this hypothesis.

Historic and intense hunting pressure precludes a solely ecological explanation of langur distribution and abundance on karst habitats, however. A similar ecological conundrum of African primate communities has been addressed by Tom Struhsaker (Struhsaker, 1999). He notes that the present-day distribution of many species may be the artifact of recent hunting, rather than the result of long-time evolution. One cannot assume that the remnants of a once widespread population have settled on preferred habitat or that the remnant populations represent normality (Lovejoy et al., 1984). Remnant habitats might best be interpreted as those habitats least favorable to the cause of the species' decline (Caughley, 1994) and unmined karst is land that is largely unusable for human agriculture or logging in Southeast Asia (Whitmore, 1984). Limestone karsts might be refuge habitats, yet contrary to predictions based on refuge habitat, *Trachypitheus leucocephalus* spend 2/3 of their time at the bottom portion of limestone blocks, not sequestered towards the karst peaks where they would be farthest away from humans (Huang et al., 2002).

Without current support for a dietary explanation, it seems probable that limestone langurs occupy limestone karst habitat primarily because they have been forced exclusively into it as a refuge from deforestation and conversion of forested valleys between karsts into rice agriculture (Li and Rogers, 2005). Additional ecological factors-including the use of caves for thermoregulation and protection from climatic conditions –are secondarily important. Several primate species use caves, at least in part, for thermoregulatory purposes (*Lemur catta*: Goodman and Langrand, 1996; *Pan troglodytes verus:* Pruetz 2001; *Papio ursinus:* Barrett et al., 2004). Huang et al. (2004) report that *Trachypithecus francoisi* in Fusui Nature Reserve, China enters caves earlier in winter than in summer, and they leave later in winter than in summer. Langurs also sometimes enter caves during the hottest part of the day, and heavy winds and rain can cause the langurs to enter caves (Huang et al., 2004). During the study period, Delacour's langurs took shelter in rock ledges and caves during rainstorms and they slept in caves more during the winter than the summer. Were non-karst habitats still available to them, there is no reason to suggest that Delacour's langurs would not have the dietary flexibility to expand their adaptive range. Unfortunately, while karst is unsuitable for agriculture, accelerated limestone blasting for cement production threatens the remaining unprotected karst areas and their fragmented langur populations.

5.5 Appendix

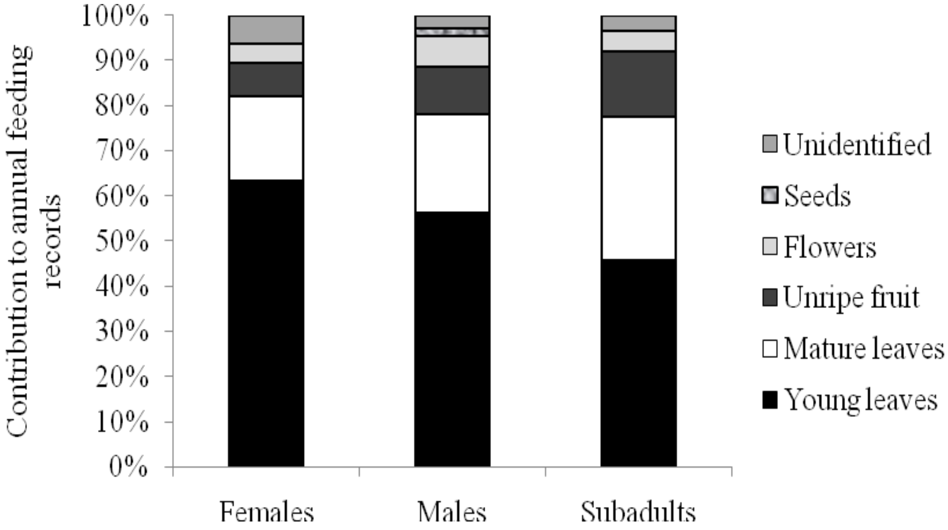

Figure 13: Feeding differences between Delcour's langur age-sex classes

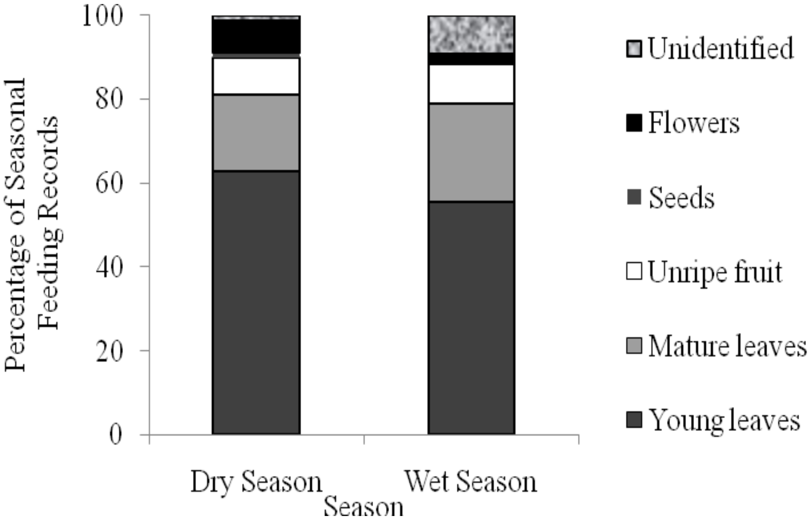

Figure 14: Seasonal feeding of plant parts

Table 20: Top 16 species' contribution (%) to monthly feeding records

	Aug 07	**Sep 07**	**Oct 07**	**Nov 07**	**Dec 07**	**Feb 08**	**Mar 08**	**Apr 08**	**May 08**	**Jun 08**	**Jul 08**
Broussonetia papyrifera	2	3.3	5.2	16.8	19.7	0	42.4	15.9	9.7	14.5	7.6
Wrightia macrocarpa	0	0	0	5.1	13.7	9.7	12.6	15.1	16.3	3.5	7.6
Alangium kurzii	6.2	17	14.9	1.3	1.6	0	6.9	5.2	14.6	11.6	19.6
Ficus microcarpa	3.2	7.3	6.9	7	0.37	0	11.7	8.8	6.8	26.4	23.3
Lantana camara	0	1.2	4.6	14	13.7	0	0	0.14	0	0	2.2
Alchornia tiliaefolia	0	0	0	8.2	3	14.5	7.1	1	0.19	0	1.8
Derris tonkinensis	1.1	1.6	0	0.81	0	24.2	0	0	7.2	1.6	0
Ipomoea bonii	0	0	2.3	10.5	6.1	0	1	0	0	0	0
Linociera verticillata	0	0	2.2	0	0	7.5	0	1.7	10.8	11.3	0.36
Diospyros mollis	0	0	0	2.6	0	3.8	2.2	3	4.4	0	3.6
Gardenia tonkinensis	0	0	0	4.8	0	0	0	0	8.1	11	0
Mallotus philippensis	0.71	1.2	0	1.9	0	0	0	3.9	6.4	3.1	2.9
Bridelia retusa	0	0	0	0	0	0	0	9.1	0	4.1	0
Debregeasia squamata	0	0	0	0	0	0	8.5	0	0.19	0	0
Hiptage lucida	0	0.93	0	0	0	0	0	4.9	0	0	0
Stephanie rotunda	0	0	0	0	0	0	1.3	2.9	2.7	2.2	3.6
Total	13.2	32.5	36.1	73.0	58.2	59.7	93.7	71.6	87.4	89.3	72.6

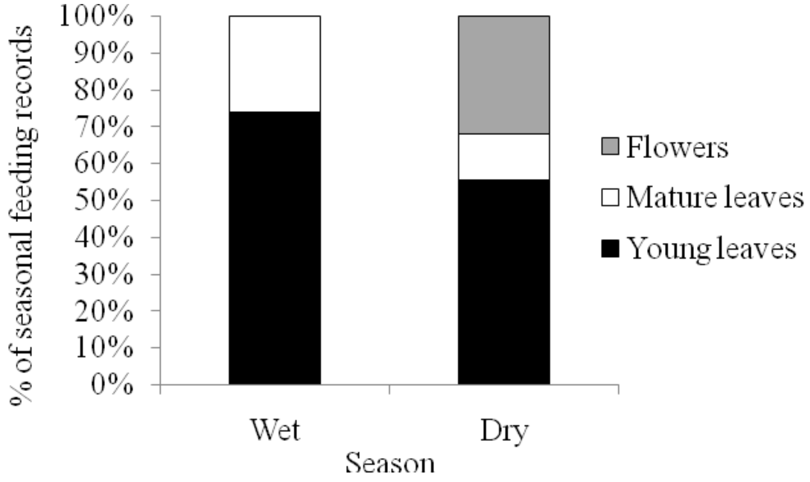

Figure 15: Seasonal consumption of *Broussonetia papyrifera*

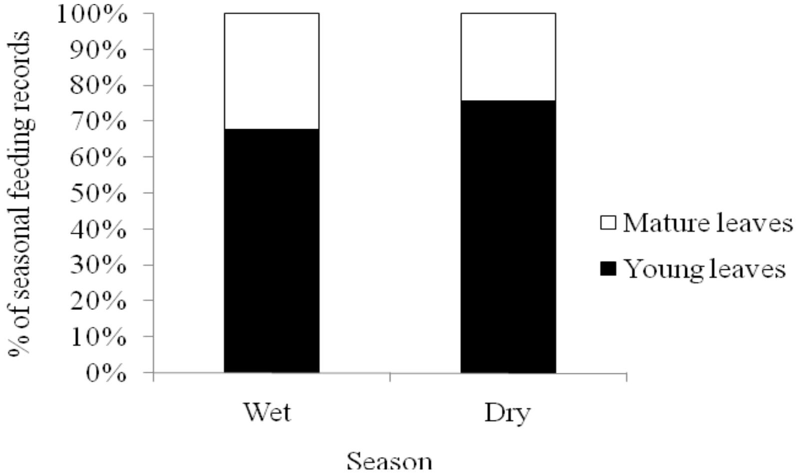

Figure 16: Seasonal consumption of *Wrightia macrocarpa*

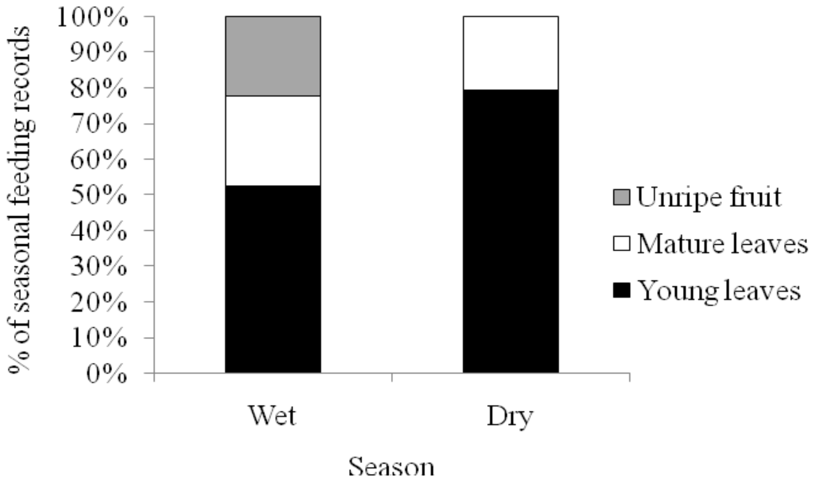

Figure 17: Seasonal consumption of *Ficus microcarpa*

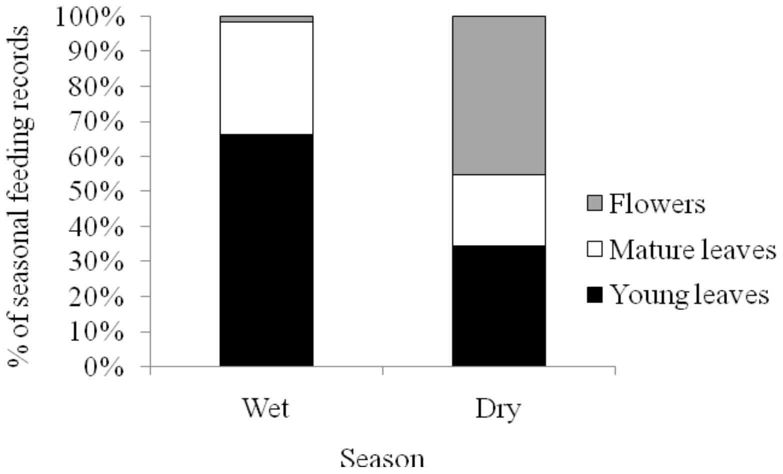

Figure 18: Seasonal consumption of *Alangium kurzii*

Table 21: Plant species and parts eaten by Delacour's langurs at Van Long Nature Reserve, June 2007-July 2008

Species	**YL**	**ML**	**UF**	**RF**	**FL**	**Bud**	**ST**	**SD**	**SH**	**FB**
Alangium kurzii	X	X			X	X				
Wrightia macrocarpa	X	X			X					
Pothos repens	X								X	
Bauhinia rubro	X									
Quisqualis indica	X				X	X				
Combretum griffithii	X									
Trophis scandens	X		X							
Ipomoea bonii	X	X			X	X	X			
Dioscorea glabra	X	X								
Diospyros mollis	X	X	X							
Mallotus philippensis	X	X	X							
Alchornia tiliaefolia	X	X								
Sapium rotundigolium	X	X								
Acalypha siamensis	X									
Bridelia retusa	X									
Bridelia sp	X									
Derris tonkinensis	X	X			X	X		X		
Homalium cochinchinense	X									
Taxillus sp			X							
Hiptage lucida	X									
Cocculus sarmentosus			X							
Stephanie rotunda	X	X	X							

Table 21, continued

Pycnarrhena lucida	X									
Ficus microcarpa	X	X	X	X						
Ficus orthoneura	X									
Maclura cochinchinensis	X		X							
Broussonetia papyrifera	X	X			X					
Linociera verticillata	X	X	X			X				
Prunus fordiana	X									
Eriobotrya bengalensis			X							
Gardenia tonkinensis	X	X	X							
Mussaenda glabra					X					X
Micromelum hirsutum	X	X			X					
Xanthoxylum sp	X									
Sterculia lanceolata	X									
Latana camara			X							
Debregeasia squamata	X									
Vitex sp	X									
Unknown (sample #14)	X									
Unknown (sample #32)	X									
Unknown (sample #39)	X									
Unknown (sample #42)	X	X								

YL=young leaves; ML=mature leaves; UF=unripe fruit; RF=ripe fruit; FL=flowers; Bud=leaf bud; ST=stem; SD=seed; SH=shoot; FB=flower bud

6. Chemistry of Plants and Soils

6.1 Introduction

Colobine monkeys of Africa and Asia are unique among primates in the complexity of their enlarged, sacculated forestomachs (Chivers, 1994). These complex stomachs serve as fermentation chambers for large quantities of anaerobic bacteria which can breakdown the cellulose-rich plant cell walls, thereby producing volatile fatty acids that colobines can absorb as energy (Kay and Davies, 1994). In addition to the energy generated through fiber fermentation, digestion of the microbes provides the major protein source for colobines (Van Soest, 1994). Forestomach fermentation allows colobines to periodically fall back on mature foliage, a plant resource on which monogastric monkeys cannot depend (Marshall and Wrangham, 2007).

Several morphological, physiological, and ecological factors appear to influence colobine leaf selection, but nutritional factors, especially leaf protein and digestibility, are among the most powerful (Kirkpatrick, 2007). For three decades, protein:fiber ratio has been recognized as a good predictor of leaf choice for relatively small mammalian herbivores, including primates (Milton, 1979). While an optimal level of fiber is needed to regulate the emptying of the colobine forestomach, fiber is inversely related to digestibility (Waterman and Kool, 1994). Chapman et al. (2002) list several studies that have supported the importance of protein and fiber in colobine leaf selection (McKey et al., 1981; Davies et al., 1988) and others that support colobine selection for plant material that is easily digested due to low fiber and polyphenolic content and high protein content (Oates et al., 1980; Waterman and Choo, 1981). As leaves age, they contain less protein and more fiber and lignin, and therefore young leaves are generally more digestible than mature ones (Baranga, 1986). The importance of protein and fiber in colobine leaf choice is further emphasized by the robust link between mature leaf protein:fiber ratio and colobine biomass across Africa and Asia (Waterman et al., 1988; Waterman and Kool, 1994).

While protein and fiber levels are of paramount importance in leaf selection, various secondary compounds may also influence selection. Phenolics are the parent group of tannins, hydrophilic polymeric phenols that precipitate starch and proteins, lower nitrogen availability, lower nutrient quality, and reduce digestion (Rhoades and Cates, 1976). Tannins sometimes have beneficial effects in the diet by decreasing bloat (a foaming of digesta in the forestomach) and binding to, precipitating, and detoxifying alkaloids (Cork and Foley, 1991; Glander, 1994), but condensed tannins bind proteins, and there by negatively influence food choice, (Feeny, 1976; Coley and Barone, 1996).

Despite extensive studies of nutritional dietary ecology among colobines, comparatively few data exist for the six limestone langur taxa of Southeast Asia (*Trachypithecus poliocephalus, T. francoisi*, *T. p. leucocephalus, T. delacouri*, *T. laotum*, and *T. l. hatinhensis*). Studies of feeding ecology in the wild have been conducted on

Trachypithecus poliocephalus leucocephalus (Huang et al., 2000; Li et al., 2003; Li and Rogers, 2006), *T. francoisi* (Zhou et al., 2006; Huang et al., 2008; Zhou et al., 2009a) and *T. delacouri* (Workman, 2010; Chapter 5), but the relationship between plant chemistry and food selection has not yet been considered for any of these species. This omission has important implications given that vegetation on limestone differs greatly in species composition and structure relative to forests with other xeric and edaphic conditions (Sterling et al., 2006). In particular, the soils of limestone formations have been described as thin, highly alkaline, sandy, dry, and low in mineral nutrients, causing high levels of plant endemism but limiting the growth of many plant species (LeGrand, 1973; McAleese and Rankin, 2003; Sterling et al., 2006). In Kalimantan, for example, limestone karst forests have roughly one-third of the plant diversity present in lowland Dipterocarp forests (MacKinnon et al., 1996; Marshall et al., 2007). Vegetation on karst is notoriously stunted, with many grasses, lithophytic plants, shrubs and small trees (Li et al., 2003; Day and Chenoweth, 2004; Liu et al., 2004). This stunted vegetation, coupled with the presumed soil conditions (thin, highly alkaline, sandy, dry, low in mineral nutrients) has been assumed to reflect plants whose leaves are well-defended by defensive compounds because they are growth-limited (Sterling et al., 2006).

Soils are a major determining factor of plant communities and soil composition has been shown to correlate with plant secondary compounds (John et al., 2007). In Uganda's Kibale National Park, generally more fertile and higher quality soils contain lower levels of leaf secondary compounds (Gartlan et al., 1980), although soil composition varies within the site (Struhsaker, 1997). McKey et al. (1978) showed that the acidic, low-nitrogen, low-phosphorous soils of Douala-Edea, Cameroon have plants with higher carbon-based defenses (phenolics) than similar vegetation of the soils in Kibale, Uganda. The effect of phenolic-defended plants on low nutrient, sandy soils is a lowering of animal abundance (Oates et al., 1990).

Poor soil environments are those high in sand, low in pH level (acidic), and low in mineral nutrients creating low fertility (Young, 1976; Oates et al., 1990; Marquis, 2005). High acidic levels (pH less than 5.5) lower nutrient availability making growth harder (Young, 1976). Leaves are therefore more costly to produce in such an environment, so plants produce higher secondary compound content, especially phenolics and tannins, to deter herbivorous predation (Janzen, 1974). In nutrient-poor environments, nitrogen levels are low yet carbon is abundant; therefore, carbon-based defenses (digestion-reducing substances) are the main type of plant defense (Rhoades and Cates, 1976). Nutrient-poor sites have more carbon-based (digestion-reducing) defenses and richer sites more nitrogen-based (toxic) allelochemics (Rhoades and Cates, 1976). In such environments, plant energy is invested in defense over growth.

Delacour's langurs are critically endangered and the largest wild population lives at Van Long Nature Reserve (VLNR) in northern Vietnam. From August 2007-July 2008 the feeding behavior of Delacour's langurs was studied and their diet was characterized as highly folivorous, eating 78% foliage annually: 59.3% young leaves and leaf buds, 20.4% mature leaves, 9.2% unripe fruit, 5.1% flowers and flower buds, 0.6% seeds, 0.3% stems, 0.1% ripe fruit, and 5% unclassified items (Workman, 2010; Chapter 5). Phenological monitoring during the study period recorded young leaves as available in every month from August 2007-July 2008, suggesting a contradiction in the literature of limited growth availability. Young leaves contributed the greatest percentage to the diet during all months and seasons (Workman, 2010; Chapter 5).

Having a radiation of leaf-eating monkeys that are so highly folivorous and found in close association with limestone habitat creates a new opportunity to reassess the degree of variation in colobine diets and food selection. I wanted to determine how protein, fiber, and phenolics (especially tannins) correlate with langur food choice. Second, I wanted to determine if the soils at Van Long can be characterized as 'poor,' having low mineral nutrients, being either highly alkaline or acidic, and sandy. Finally, I wanted to compare how soil characteristics and plant chemistry at Van Long differ from that at other colobine sites.

6.2 Methods

6.2.1 Study Site and Behavioral Data Collection

Research was conducted at the Dong Quyen karst mountain of Van Long Nature Reserve (20°20′55″N, 105°48′20″E) in Ninh Binh Province, northern Vietnam. Characteristics of the study site were described in Chapters 3 and 5. To determine which foods Delacour's langurs were eating and not eating, I observed focal individuals using the methods described in Chapters 3 and 5 and Workman (2010).

6.2.2 Plant Sample Collection and Plant Chemistry

Plant feeding samples were collected at the end of a morning or evening observation session, when groups had moved out of view. Most plants were short enough that tree-climbing was usually not necessary. A sample from the plant that was eaten (e.g. the young leaves of a small tree) was collected as well as a matching phenophase sample from a plant that was next to the eaten plant, but not consumed. If there was a plant of the same species close by, a sample from that plant was collected. While the species consumed is reported here, the focus was less on the plant species eaten than on the plant individual that was eaten.

Intraspecific variability in the nutritional content of primate foods has been well documented (Chapman et al., 2003), but the aim of this study was not to determine the nutritional content of certain species on which Delacour's langurs fed, but rather on the differences between plant individuals at a given time. The steep topography of the karst habitat precluded me from accessing certain areas and therefore the sample set presented is limited to those plants which I could safely access. Eaten and uneaten samples had fresh masses between 80 g and 1047 g, with a mean of 535 g and SD of 116 (*n* =51 eaten samples (40 young leaves, 10 mature leaves, 1 unripe fruit; *n* = 50 uneaten samples (40 young leaves, 10 mature leaves).

Samples were transported in bags to the Van Long Ranger Headquarters and weighed within two hours of collection, dried in the shade over a period of days or weeks (depending on weather), and then kept at room temperature until analysis. Dried samples were taken to Ms. LanAnh at the Hanoi University of Science for transport to one of two testing facilities: 1) Food and Chemical Microbiology and Food Testing Laboratory of Quality Assurance and Testing Center Number, Hanoi; 2) National Institute of Animal Husbandry, Hanoi. Eaten and uneaten samples were analyzed for crude protein, neutral detergent fiber (NDF), condensed tannin, total phenolics, crude ash, and water content. Samples were ground dry in a Wiley laboratory mill and passed through a 1 mm wire screen (Chapman et al., 2002). All samples were dried to a constant weight of 100^0C and all results are provided on a dry matter basis.

Crude protein content was assessed using the Kjeldahl method (Horowitz, 1970). Total nitrogen content was first measured and then used to estimate the crude protein level (protein content = nitrogen * 6.25: Maynard and Loosli, 1969). Fiber (Neutral detergent fiber (NDF)) was measured by following the methods described in van Soest (1963). NDF is a measure of the structural components in plant cells (i.e. lignin, hemicellulose and cellulose), but not pectin. NDF was measured because it is a more reliable measure of the fibrous component in the diet (compared to ADF) but we realize that not having ADF makes our results difficult to compare with other studies. Total phenolics were analyzed by the Folin-Denis method (Swain and Hillis, 1959). Tannins were determined using the $KMnO_4$ titration method (Tempel, 1982).

6.2.3 Soil Sample Collection and Soil Chemistry

Soil samples were collected from along two established phenology transects within the home range of the study groups in August 2007 and February 2008. Transect One is 230 meters long, from zero to 92 meters elevation. Transect Two is 361 meters long, from zero to 124 meters elevation. Ten soil samples (five from each transect) were collected about every 25 meters along both transects, to account for the change in elevation up the mountain. Because much of the karstic habitat is exposed rock with scant soil, soil frequently had to be collected several meters away from the transects to sample enough soil. I tried to use a one-piece step probe, but the rocks and shallow dirt prevented collecting with it because it could not penetrate deep enough. Instead, I wore gloves to brush away the topsoil as well as leaves, twigs, rocks, before collecting by hand. Soil was put into small plastic sampling bags and transported to the Van Long Ranger Headquarters. Large pieces of debris were taken out of the samples and sundried.

Once dry, the samples were put into individually labeled plastic bags and mailed to the United States Plant Inspection Station in Hawthorne, CA to undergo heat treatment. Brookside Laboratories Inc. in Brookside, OH then analyzed the soil for pH following the methods of Watson and Brown (1998); several extractable nutrients (Ca, Mg, K, Na, P, Zn, Fe, and Mn) following the methods of Warncke and Brown (1998) and Mehlich (1984); total Carbon, total Nitrogen, and C/N Ratio following Combs and Nathan (1998); texture (total sand, silt and clay) using the hydrometer method (ASTM, 2002). Descriptive results of soil analyses were mostly given in ppm (mg/kg). In order to compare with other sites, results were converted into mmole/kg. To do this, the atomic weight of each compared element was multiplied by 1,000. The following formula was then used (Ca as example): X mg Ca/1 kg soil * 1 mole Ca/40078 mg Ca * 1000 mmole Ca/1 mole Ca (with X representing the sample ppm). The soil collected in February 2008 was not allowed to be shipped outside of the country for analysis, and therefore only results from the soil collected in August 2007 are reported.

6.2.4 Statistical Analyses

Differences in plant chemistry (crude protein, NDF, total phenolics, condensed tannins, water, ash content) were analyzed between several groups. First, I compared eaten leaves (N=50) vs. uneaten leaves (N=49). Second, because 89% of rainfall occurred between May-October, I compared leaves eaten during the wet season (May-October: N=36) with leaves eaten in the dry season (November-April: N=14). Third, from August 2007-July 2008, young leaves dominated the Delacour's langurs' diet monthly, seasonally, and annually. I therefore compared young leaves (N=40) vs. mature leaves (N=10). Fourth, there were four plant species that accounted for 55% of the Delacour's langurs' diet from August 2007-July 2008 and therefore were the most frequently consumed species for Delacour's langurs in terms of total percentage of feeding records: *Broussonetia papyrifera, Alangium kurzii, Ficus microcarpa*, and *Wrightia macrocarpa.* I compared leaf samples of these frequently consumed species (N=23) with leaves of eaten plants that were less frequently consumed (N=27). Finally, I analyzed leaves eaten by adult males (N=18) vs. adult females (N=30). Females with dependent young and subadults were not compared with adult male and females due to low sample sizes. All differences were analyzed using a non-parametric Wilcoxon test (the equivalent of the non-parametric Mann-Whitney *U* test) using open software R 2.7.1 for Windows.

6.3 Results

6.3.1 Plant Chemistry

6.3.1.1 Eaten versus Uneaten Leaves

Leaves eaten by Delacour's langurs (N=50) had a higher protein:fiber ratio than leaves not selected (N=49) (mean = 0.42 +/- 0.18 vs. mean = 0.31 +/- 0.16; P < 0.01) (Table 22). Leaves eaten and uneaten were not statistically different in protein (mean = 12.04 +/- 6.88 vs. mean = 10.58 +/- 5.82; P=0.13), fiber (mean = 32.47 +/- 18.62 vs. mean = 38.18 +/- 21.09; P=0.06), total phenolics (mean = 2.13 +/- 2.17 vs. mean = 1.52 +/- 1.68; P=0.09), tannins (mean= 6.36 +/- 4.81 vs. mean = 4.81 +/- 3.92; P=0.08), water (mean = 80.88 +/- 5.74 vs. mean = 78.92 +/- 8.53; P=0.36), or ash content (mean = 16 +/- 6.97 vs. mean = 19.53 +/- 9.18; P=0.11).

Table 22: Mean values of eaten (N=50) and uneaten leaves (N=49). Standard deviations in parentheses. * Significance P<0.01

	Eaten leaves	Uneaten leaves
CP:F*	0.42 (0.18)	0.31 (0.16)
Protein	12.04 (6.88)	10.58 (5.82)
Fiber	32.47 (18.62)	38.18 (21.09)
Tannins	6.36 (4.81)	4.81 (3.92)
Phenolics	2.13 (2.17)	1.52 (1.68)
Water	80.88 (5.74)	78.92 (8.53)
Ash	16 (6.97)	19.53 (9.18)

6.3.1.2 Plant Chemistry in Relation to Dietary Contribution

Feeding samples from the four most frequently consumed species in the Delacour's langurs' diet (N=23) contained lower amounts of condensed tannins (mean=3.41 +/- 1.79 vs. mean = 8.78 +/- 5.18; P< 0.01) and total phenolics (mean = 1.19 +/- 1.08 vs. mean = 2.9 +/- 2.52; P< 0.01) compared to the less frequently consumed food species (N=27). Further, the protein:fiber ratio of foods that were more frequently consumed was higher than that for less frequently consumed foods (mean = 0.52 +/- 0.16 vs. mean = 0.35 +/- 0.16; P< 0.01). Differences between these two food classes were not significant for water (mean = 82.82 +/- 4.16 vs. mean = 79.28 +/- 6.4; P= 0.07), crude protein (mean = 12.78 +/- 7.45 vs. mean = 11.53 +/- 6.34; P=0.42), ash (mean = 14.64 +/- 5.81 vs. mean = 16.06 +/- 8.54; P=0.3), fiber (mean = 30.93 +/- 18.54 vs. mean = 33.95 +/- 18.94; P=0.48).

6.3.1.3 Leaf Stage Differences in Plant Chemistry

Samples of young (N=40) and mature leaves (N=10) eaten by Delacour's langurs did not differ in their content for any of the analyzed constituents (Table 23): protein (mean = 12.13 =/- 6.92 vs. mean = 11.94 +/- 6.74; P= 0.91), fiber (mean = 34 +/- 19.53 vs. mean = 26.17 +/- 13.28; P=0.22), total phenolics (mean = 2.25 +/- 2.38 vs. mean = 1.55 +/- 0.87; P=0.75), condensed tannins (mean = 6.01 +/- 4.74 vs. mean = 7.79 +/- 5.1; P=0.28), water (mean = 81.19 +/- 5.51 vs. mean = 79.61 +/- 6.75; P=0.57), ash (mean = 16.24 +/- 6.89 vs. mean = 16.04 +/- 7.82; P=0.88), protein:fiber ratio (mean = 0.41 +/- 0.19 vs. mean = 0.46 +/- 0.16; P=0.53).

Table 23: Nutrient and defensive compound content in eaten plant samples from Van Long Nature Reserve, August 2007-July 2008. Parentheses denote percentage contribution to annual feeding records.

Family and species	Plant part	N	CP (%DM)	NDF (%DM)	CT (%QTE)	TP (%DM)	Water	Ash (%DM)	CP:F
Alangraceae									
Alanguum kurzii (11.1)	YL	4	14.87	28.88	3.28	1.38	84.49	13.73	0.51
	ML	4	16.89	38.26	5.33	1.51	80.44	19.56	0.45
Apocynaceae									
Wrightia macrocarpa (13.4)	YL	3	2.99	4.18	3.85	0.49	85.77	10.82	0.73
Caesalpinaceae									
Bauhinia rubro (0.08)	YL	1	9.4	52.13	11.3	9.49	72.3	27.7	0.18
Combretaceae									
Combretum griffithii (0.03)	YL	1	1.63	5.83	21.32	6.39	81.99	9.9	0.28
Convolvulaceae									
Ipomoea bonii (4.3)	YL	2	18.6	37.84	13.36	1.42	86.91	13.1	0.5
Ebenaceae									
Diospyros mollis (2.4)	ML	2	6.49	19.72	7.2	1.11	72.43	19.47	0.37
Euphorbiaceae									
Alchornia tiliaefolia (6.7)	ML	1	20.22	23.28	18.84	2.2	89.42	10.58	0.87
Mallotus philippensis (1.9)	ML	1	2.37	6.07	1.6	0.27	86.31	10.02	0.39
Fabaceae									
Derris tonkinensis (4.8)	YL	4	15.6	44.63	9.23	2.12	80.55	6.64	0.42
	ML	1	4.83	14.84	9.5	2.65	70.75	5.58	0.33
Moraceae									

Table 23, continued

Broussonetia papyrifera (22.2)	YL	7	16.61	28.47	2.29	0.79	82.31	17	0.59
Ficus microcarpa (9.2)	YL	6	9.48	37.17	2.98	2.23	79.52	16.59	0.24
Maclura cochinchinensis (0.34)	YL	1	13.16	29.17	4	6.08	83.1	16.9	0.45
Oleaceae									
Linociera verticillata (2.7)	YL	2	4.47	46.08	2.82	3.02	66.41	19.24	0.1
Rubiaceae									
Gardenia tonkinensis (2.2)	YL	3	7.89	23.53	11.66	5.94	79.48	16.29	0.35
	ML	1	11.4	25.09	12.25	2.14	82.98	17.02	0.45
Rutaceae									
Zanthoxylum sp (0.03)	YL	1	12.7	44.56	4.17	0.53	6.09	23.91	0.29
Uderbenaceae									
**Latana camara* (7.2)	UF	1	7.13	69.78	2.78	3.13	92.92	7.08	0.10
Verbenaceae									
Vitex sp (0.23)	YL	1	15.52	47.01	13.9	1.01	73.15	26.85	0.33
Sample #14 (0.17)	YL	1	20.22	40.2	4.34	0.58	84.8	15.2	0.5
Sample #32 (0.03)	YL	1	12.85	46.34	8.8	3.01	80	20	0.28
Sample #39 (0.03)	YL	1	14.6	42.97	10.42	1.51	82.33	17.67	0.34
Sample #42 (0.03)	YL	1	16.5	48.86	2.58	0.33	86.22	13.78	0.34

6.3.1.4 Seasonal Variation in Plant Chemistry

Foods that Delacour's langurs ate during the wet season (N=36) contained higher amounts of fiber than foods eaten during the dry months (N=14) (mean = 37.54 +/- 20.69 vs. mean = 23.03 +/- 15.49; P< 0.02). However, we found no differences in protein (mean =

13.16 +/- 6.74 vs. mean = 9.28 +/- 6.43; P=0.07), total phenolics (mean = 2.41 +/- 2.4 vs. mean = 1.38 +/- 1.1; P=0.19), condensed tannins (mean = 5.83 +/- 4.71 vs. mean = 7.74 +/- 4.96; P=0.09), water (mean = 80.91 +/- 5.49 vs. mean = 80.81 +/- 6.55; P=0.89), ash (mean = 16.79 +/- 6.92 vs. mean = 14.64 +/- 7.21; *p* = 0.23), or protein:fiber ratio (mean = 0.41 +/- 0.18 vs. mean = 0.41 +/- 0.18; P=0.59).

6.3.1.5 Sexual Preference in Chemistry of Plant Part Eaten

The foods eaten by male (N=18) and female (N=30) Delacour's langurs did not differ in their protein content (mean = 14.47 +/- 6.26 vs. mean = 10.71 +/- 7.09; P=0.05), fiber (mean = 36.23 +/- 15.76 vs. mean = 28.55 +/- 20.18; P=0.27), total phenolics (mean = 2.29 +/- 2.45 vs. mean = 1.96 +/- 2.14; P=0.66), condensed tannins (mean = 4.18 +/- 2.63 vs. mean = 7.29 +/- 5.39; *P*=0.06), water (mean = 81.77 +/- 5.48 vs. mean = 81.39 +/- 5.85; P=0.93), ash content (mean = 17.46 +/- 5.91 vs. mean = 15.72 +/- 6.94; P=0.38), or the protein:fiber ratio (mean = 0.44 +/- 0.17 vs. mean = 0.42 +/- 0.19; P=0.38).

6.3.2 Soils

Soil chemistry and composition on the Dong Quyen Mountain of VLNR differ slightly between transects (Table 24). Averaging samples from the two transects, the soil is 40.1% clay, 43.7% silt, and 15.71% sand. The mean pH is 7.0. Organic matter content is 30.75%. The percentage of calcium in the soil is 89.5%, with much smaller amounts of manganese (3.73%), potassium (0.97%), sodium (0.39%), and other (5.41%). There is 20% carbon and 2.4% nitrogen in the soil, with a carbon: nitrogen ratio of 7.8.

Table 24: Descriptive statistics of soil analysis from Dong Quyen Mountain, Van Long Nature Reserve, Vietnam

Soil analysis	Transect 1	Transect 2
pH	7 (6.9-7.2)	6.9 (6.8-7)
Sand %	24.7	6.7
Silt %	45.8	41.6
Clay %	29.5	51.6
Organic Matter (%)	26.19 (6.88-53.55)	35.33 (13.93-50.45)
Carbon (%)	17.5 (1.96-36.95)	22.8 (6.52-32.92)
Nitrogen (%)	1.8 (0.38-3.07)	3 (1.02-4.2)
P (mg/kg)	212 (35-377)	311.2 (69-503)
K (mg/kg)	207.6 (109-270)	256.4 (199-299)
Ca (mg/kg)	13343 (7084-19000)	10665.8 (8605-12200)
Mg (mg/kg)	272.8 (102-680)	275.2 (140-444)
Na (mg/kg)	63 (40-92)	47 (28-73)
Fe (mg/kg)	38.8 (28-61)	50.2 (28-66)
Zn (mg/kg)	17.61 (8.36-27.56)	31.76 (7.86-43.07)
Mn (mg/kg)	532.4 (102-860)	502.8 (153-954)

6.4 Discussion

6.4.1 Chemistry of Delacour's Langur Food Choice and Comparisons with Other Colobines

Individually, neither protein nor fiber influenced what langurs ate. The fiber levels of eaten leaves in this study were lower than those of other sites (Table 25). The leaves eaten by Delacour's langurs at Van Long contain less than half the protein of leaves eaten by guerezas at Kakamega, Kenya (Fashing et al., 2007a). At Kakamega, protein content was the primary factor determining whether or not guerezas consumed specific leaf items, with eaten leaves at or above a protein threshold of 14% dry matter

(Fashing et al., 2007a). At Van Long, protein content did not differ between eaten and uneaten leaf items. Further, protein content of eaten leaves averaged 12% dry matter, with several leaf items containing protein levels far below that.

Table 25: Neutral detergent fiber (NDF) and protein levels for young (YL) and mature (ML) leaves consumed by African and Asian colobines (Modifed from National Research Council, 2003; * NDF values determined by adding 10% to ADF values)

Species	NDF	Protein	Plant part	Citation
Colobus guereza	48.0	23	mean- leaves	Fashing et al., 2007
*Presbytis johnni**	38.1		mean- YL	Oates et al., 1980
	41.6		mean- ML	
*Colobus badius**	38.8		mean- YL	Choo et al., 1981
	48.4		mean- ML	
*Colobus satanus**	58.6		mean- YL	McKey et al., 1981
	70.8		mean- ML	
*Nasalis larvatus**	44.4		mean- YL	Yeager et al., 1997
	63.9		mean- ML	
Trachypithecus delacouri	38.0	12.2	mean- YL	this study
	33.4	10.4	mean- ML	

While low compared to guerezas at Kakamega, Delacour's langurs are meeting the 7-11% protein (of dry matter) that primates need for maintenance and growth (Oftedal, 1991). Delacour's langurs at VLNR are also eating leaf items which are above the critical protein needed for ruminants to maintain positive nitrogen balance (4-8% dry weight) (Milton, 1979). Oftedal (1991) states that primate populations need to consume protein at 14% dry matter to sustain reproduction. Delacour's langurs are not quite meeting this threshold; however, the population on Dong Quyen Mountain at VLNR has doubled in 9 years (~35 langurs in 2000, ~ 70 langurs in 2009). It appears, therefore, that langurs are not limited in sustaining reproduction and are possibly receiving additional protein from food sources that we did not sample. Further, because Van Long has both evergreen and deciduous species, it is possible that- as at Kibale National Park, Uganda- the forest never reaches a very low nutrient value and colobines are not nutritionally stressed, allowing for quick population rebound (Baranga, 1986).

At Kibale, *Colobus guereza* chose young leaves that had more protein and higher protein/fiber ratios than mature leaves, although the two leaf stages did not differ in secondary compound content (Chapman et al., 2004). The preference for leaves with higher protein/fiber ratios also held at Van Long and young leaves had slightly higher protein content than mature leaves, although the difference was not significant. In Southeast Asian habitats where Dipterocarpaceae is abundant, Leguminosae- which is protein-rich compared to other plant families- tend to be rare and vice versa (Waterman et al., 1988). Neither of these families is abundant on Dong Quyen Mountain, and in fact no plant family or species dominates the flora at VLNR. The lack of protein-rich Leguminosae could be one factor contributing to the lower protein levels consumed by Delacour's langurs.

It has been suggested that tannin concentrations may be of minor significance to primates (Oates et al., 1980). While tannin content did not differ between leaves eaten and uneaten during our study, total phenolic content and the condensed tannin content are lower in the four most frequently eaten species (which comprised 55% of the diet) compared to the species that comprise less of the annual diet. Because the protein and fiber levels between the more and less frequently eaten species did not differ, it suggests that defensive substances (phenolics and tannins) influence the percentage contribution of certain species to the annual diet. However, because I only analyzed a limited number of micronutrients, I cannot rule out the influence of other intrinsic plant factors on selection. It may also be that if Delacour's langurs are always walking a fine protein edge they are more tannin sensitive to avoid precipitating additional protein out of their diet.

6.4.2 Should the Soils at Van Long Be Characterized as 'Poor'?

Poor soil environments are those high in sand, low in pH level, and low in mineral nutrients (Oates et al., 1990; Marquis, 2005). Given these measures, soils at VLNR should not be considered poor. For example, low fertility at Tiwai is likely produced by slightly acidic (pH 4.3) and sandy (77.1%) soils (Table 26). However, soils at Van Long are thin with little surface water, features that are poor and likely promote stunted vegetation. The edaphic nutrient content at Van Long is also markedly different from African sites with colobine monkeys. For example, soils on Dong Quyen Mountain are similar to Kibale National Park, Uganda in pH (7 and 6) and sand content (15.6%, 15.7%). Soil nutrients become less available at a pH below 5.5 and above 8.0, (Young, 1976). At a pH of 7, the Van Long soils are neutral. Van Long soils are also similar to

Kibale in silt and clay content. However, the limestone soils at Van Long differ sharply in nutrient content from Kibale, Tiwai, and Douala-Edea. Van Long has a very high level of the essential nutrient phosphorous and higher levels of potassium and magnesium compared to other sites. Van Long soils also contain extremely high amounts of calcium. Limestone has been described as containing toxic levels of calcium (McAleese and Rankin, 2003), but excessive calcium levels are rarely detrimental to plant growth except when associated with high pH, when the uptake of other nutrients may be reduced (Vitosh et al., 1994). High levels of both calcium and pH at Van Long may limit the uptake of some nutrients by plants here.

Table 26: Mechanical and chemical properties of soils from Tiwai, Douala-Edea, and Kibale Forest (Oates et al., 1990) compared to Van Long Nature Reserve. * 15 samples for sand, silt, clay; 3 samples for chemistry

	Van Long	**Tiwai**	**Douala Edea**	**Kibale**
Sample *n*	10	22	34	15, 3*
pH	7	4.3	3.4	6
Sand (%)	15.7	77.1	84.8	15.6
Silt (%)	43.7	14.3	11.8	39.1
Clay (%)	40.6	8.7	3.3	45.3
P (mg/kg)	261.6	4.5	22.4	16
K (mmol/kg)	5.93	0.17	2.54	3.15
Ca (mmol/kg)	299.5	1.97	2.49	22.75
Mg (mmol/kg)	11.28	0.22	1.42	9.17

Comparing the plant community chemistry of primate sites in Uganda and Cameroon, plant phenolic metabolites and fiber levels are higher in Cameroon than

Uganda whereas alkaloids and protein levels were higher at Uganda than Cameroon (Waterman, 1986). Gartlan et al. (1980) asked what was available in the site and what the forests provided chemically. My study focused on which aspects of plant chemistry influenced selection at a given time based on what animals ate and didn't eat and the protein:fiber ratio in their diet. Future research at Van Long should focus on collecting community level protein, fiber, and secondary metabolite levels. Such information is needed to further clarify relationships between nutrient content and feeding selectivity based on total environmental availability. Such analysis will also permit more complete comparisons with previous studies (Gartlan et al., 1980; Waterman and McKey, 1989; Oates et al., 1990; Waterman, 1996).

Protein-fiber ratio has been a robust indicator of colobine biomass. The collection of community-level plant data at Van Long will expand colobine biomass comparisons across Africa and Asia. However, explaining primate biomass using the protein:fiber ratio will be misleading if populations are not at carrying capacity (Chapman et al., 2004). For the monophyletic limestone langur species of northern Vietnam, southern China, and eastern Laos, intense hunting pressure precludes a solely ecological explanation of their distribution and abundance on karst habitats. Anthropogenic effects of hunting, habitat alteration and fragmentation, and deforestation on primate communities have in fact been so pervasive and severe for the last 50 years that their consideration in any ecological analysis is required (Peres, 1999; Struhsaker, 1999; Tutin and White, 1999). One cannot assume that the remnants of a once widespread population have settled on preferred habitat or that the remnant populations represent normality (Lovejoy et al., 1984). Remnant habitats might best be interpreted as those habitats least favorable to the cause of the species' decline (Caughley, 1994). Given this consideration, a focus on proximate factors influencing langur food choice was appropriate for this study.

7. Activity Budget

7.1 Introduction

Although edible leaves are not ubiquitous and are patchily distributed (Sayers and Norconk, 2008), folivores tend to spend less time feeding and moving and more of their time resting compared to frugivores and insectivores (Clutton-Brock and Harvey, 1977). Partly due to their high degree of folivory, colobines, as a group, are among the least active of all primates (Fashing, 2007).

Temporal and quantitative food availability, group size, forest type and degree of continuity, the activities of neighboring conspecific groups, and the activities of humans are factors that influence colobine activity budgets (Oates, 1977; Boonretana, 2000; Fashing, 2001b; Teichroeb et al., 2003; Ding and Zhao, 2004; Harris and Chapman, 2007; Snaith and Chapman, 2007; Grueter et al., 2008; Teichroeb and Sicotte, 2008). Though previously not considered to be, data show that colobines contend with the same socioecological constraints as frugivores, including large group size, resource depletion, and feeding competition (Fashing et al., 2007b; Snaith and Chapman, 2007; Grueter et al., 2009a), all of which affect colobine activity budgets.

Activity budgets of colobine groups living in fragmented versus continuous forest seem to either not differ (Onderdonk and Chapman, 2000) or differ based on food quality, not habitat size (Wong and Sicotte, 2007). The activity budgets of red colobus and black and white colobus in fragmented and continuous forests were similar, but with increased resting in fragments (Chapman et al., 2007). Other studies have suggested that feeding and travel time increase with decreased habitat quality (Menon and Poirier, 1996). Lower quality foods or lower food availability may also force primates to travel longer (more time spent in travel) or farther (increase in day length) to meet all their feeding requirements (Onderdonk and Chapman, 2000; Gillespie and Chapman, 2001). However, *Colobus polykomos* on Tiwai Island and *Colobus satanus* in Gabon show the opposite pattern, increasing their travel length and range when preferred dietary items were *most* abundant (Dasilva, 1992; Fleury and Gautier-Hion, 1999). Lack of food availability has been shown to cause both longer ranging (*Colobus satanus, C. angolensis),* shorter ranging (*C. satanus*) and no difference (*C. guereza*) for colobines (Snaith and Chapman, 2007). Another limestone langur, *Trachypithecus francoisi*, conserved energy by traveling less when preferred foods were not available (Zhou et al., 2009a) yet *Nasalis larvatus* showed the opposite pattern (Matsuda et al., 2009a).

Van Long Nature Reserve is essentially island habitat, given that the shallow wetland fragments limestone blocks from one another. Because the data on how habitat quality and food availability affect colobine activity budgets are conflicting and the feeding ecology of Delacour’s langurs was unknown at the start of this study period, I made only one specific prediction for the activity budget of Delacour’s langurs at VLNR. I expected that Delacour’s langurs, like other colobines, would spend the majority of their time resting throughout the study period. I made no specific predictions for seasonal changes in activity budget.

7.2 Methods

7.2.1 Activity Budgets of Delacour's Langurs

I collected data on activity patterns during continuous focal animal follows (Altman, 1974). I collected data on adult males, adult females, females with dependent young, and subadults. I recorded behaviors in the categories of *Feed*, *Travel*, *Rest*, *Social*, and *Drink* (Table 6). Social behaviors included grooming, play, mounting, and sexual behaviors (Table 6). Because *Drink* accounted for less than 1% of the langurs' annual activity budget, *Drink* was combined with *Feed* for analyses. I also noted when a focal animal was *Out of View*. If two activities were happening at once, the following rules applied. If a focal was feeding and traveling, feeding takes priority (i.e. if there was food in the hand while traveling, the animal was scored as feeding). If a focal was traveling and socializing, socializing was recorded. If a focal was feeding and socializing, feeding was recorded.

Despite Clutton-Brock's (1973) assertion that colobine feeding bouts are easily determined because colobines never feed while traveling, other researchers have noted difficulty in determining travel from foraging (travel used during feeding) (Gebo and Chapman, 1995b). Following Gebo and Chapman (1995b), I scored travel within a tree as feeding and travel between trees as travel (Gebo and Chapman, 1995b). A similar differentiation was not made for travel versus feeding on rocks, because there was no easy way to divide within versus between rock movements. Therefore, although difficult, I did my best to accurately determine the context of the travel when langurs were on rocky substrates. Feeding and traveling were therefore scored, but 'foraging' per se was not.

Activity budgets for each age/sex class were calculated as a proportion of the total time of activity records. To calculate activity budgets, I computed the total proportion of time of each of the four activities (*Feed* included *Drink* for analyses) for each day, with *Out of View* excluded. These daily values were then used to calculate monthly activity budgets. The annual activity budgets represent the average of the monthly activity budgets.

7.3 Results

7.3.1 Activity Budgets

Overall, resting dominated the activity budget, accounting for 61% of the time. Feeding was the next most frequent activity at 29% and socializing and traveling were the least frequent activities at 6% and 4%, respectively. Because drinking accounted for less than 1% of activities, drinking is included with feeding in all figures and tables. The annual activity pattern varied only slightly between months and seasons (Figures 19, 20). More resting and less feeding occurred in July 2007 and March 2008, but because these are months of both the wet (July) and dry (March) seasons, no pattern emerges.

February, March, June, and July of 2008 are the months with the highest frequency of social activity, whereas November and December, 2007 and April 2008 are the months with the greatest percentage of time spent feeding. Percentage of time spent in travel shows no monthly or seasonal pattern, as June and July are the months with the highest (2007) and lowest (2008) time spent traveling. Langurs travel slightly more in the wet season.

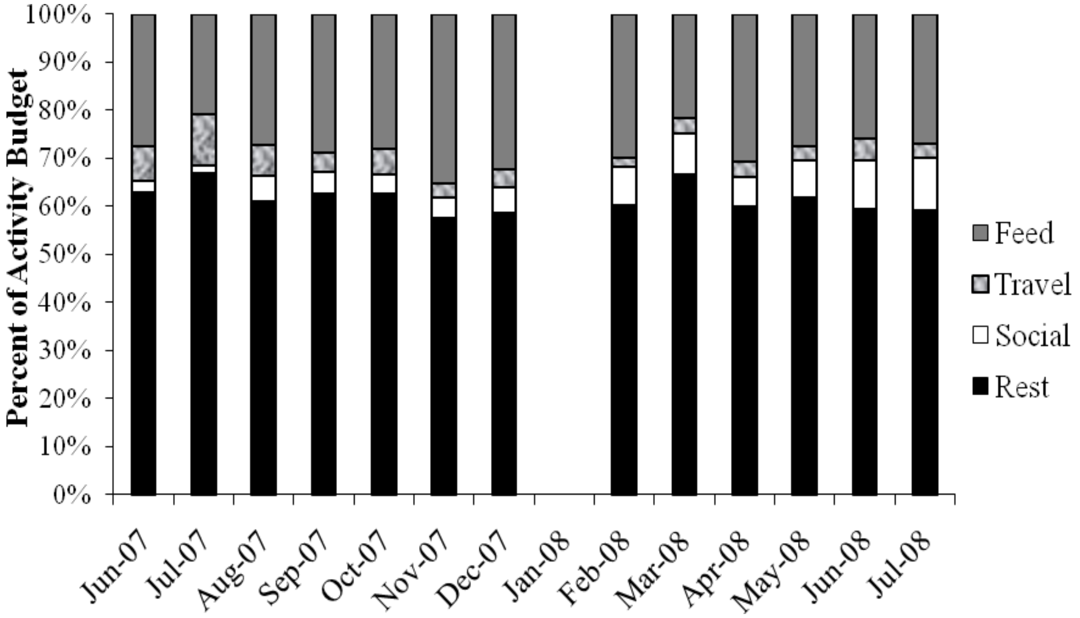

Figure 19: Monthly activity budget for Delacour's langurs at Van Long Nature Reserve, June 2007-July 2008

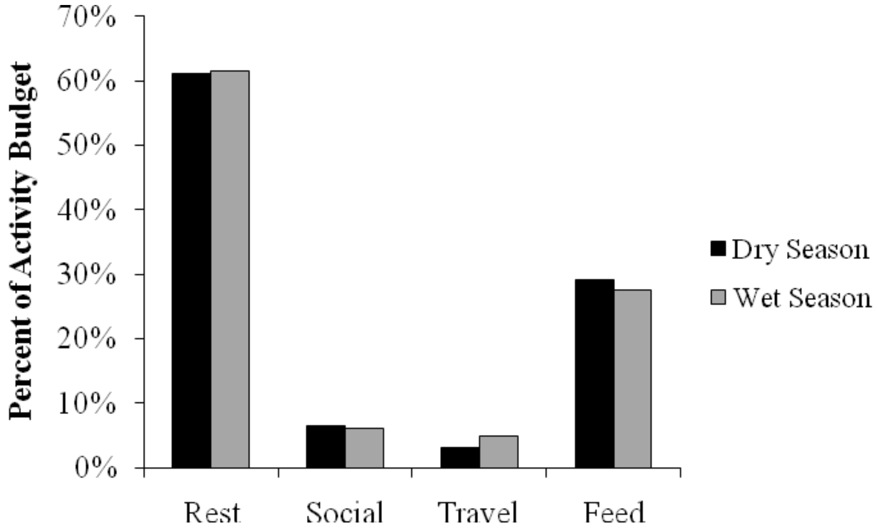

Figure 20: Seasonal activity budgets of Delacour's langurs at Van Long Nature Reserve, June 2007-July 2008

Between sexes, females spent more time socializing and feeding and males spent more time resting (Figure 21). There was no difference between the sexes in frequency of travel. Social behavior largely consisted of grooming behavior. Females groomed males, subadults and infants, but most often groomed other females. In the unimale langur groups, males never were observed grooming females. In the two-male Valley group, however, both males groomed one another, but neither was observed grooming the female or subadult.

Males often sat as a sentry while females fed or socialized below or behind him, a behavior also noted for the Hatinh langur in Phong Nha-Ke Bang National Park, Vietnam (Haus et al., 2009). Males often sat on prominent rocks in the habitat, looking to adjacent groups (Figure 22). Group ranges overlapped at VLNR and males often performed the act of sentry along these undefined borders. Sometimes males of neighboring groups would sit at distances of 50 - >200 meters apart and look towards each other. The sight of a neighboring group would cause a male to exhibit a "bounding display," wherein the male bounded quadrupedally across the habitat, jumping on rocks (mostly) and emitting a "hoot" sound. On rare occasions, the presence of a neighboring male would precipitate a chase. Chases normally took place within the overlap zone of home ranges.

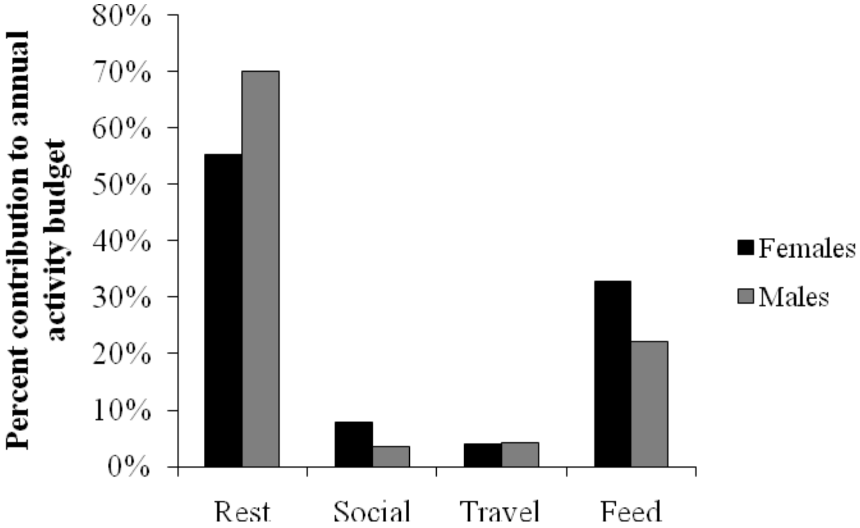

Figure 21: Activity budgets of male and female Delacour's langurs, June 2007-July 2008

Figure 22: Males often sit as sentry on prominent rocks

7.4 Discussion

7.4.1 Activity Budget

Folivorous colobine monkeys are well-known for spending copious amounts of the day resting, a strategy that minimizes energy expenditure and permits digestion of fibrous plant material (Oates, 1987; Kirkpatrick, 2007). Delacour's langurs spent 61.3% of their day resting, 28.2% feeding, 6.3% socializing, and 4.2% traveling, similar to that of other African and Asian colobines, including other limestone langurs (Table 27). Delacour's langurs are- along with *Colobus guereza*- some of the least active colobines for which activity budget data are available (Fashing, 2001b).

Table 27: Activity budgets of Asian and African colobines

Species	Site	R	F	T	S	Source
Trachypithecus delacouri	Van Long Nature Reserve, Vietnam	61.3	28.2	4.2	6.3	this study
T. poliocephalus leucocephalus	Fusui, China	50	13	18[a]	18	Li & Rogers, 2004
T. p. leucocephalus	Fusui, China	74	17	11		Huang et al., 2003
T. francoisi	Nonggang, China	51.5	23.1	17.3	7.5	Zhou et al., 2007
Rhinopithecus bieti	Tacheng, Yunnan, China	33	35	15	13	Ding & Zhao, 2004
R. roxellana	Qinling Mountains, China	36.2	35.8	22.9	5.1	Guo et al., 2007
Nasalis larvatus	Menanggul River, Sabah, Malaysia	76.5	19.5	3.5		Matsuda et al., 2009
Presbytis potenziani	Mentawai Islands, Indonesia	48	26	24	2[b]	Fuentes, 1996
Procolobus tephrosceles	Kibale, Uganda	38	45	9	8	Struhsaker, 1975
Colobus guereza	Kibale, Uganda	57	20	5	11	Oates, 1977
C. guereza	Kakamega, Kenya	63.3	25.6	2.8	7.8	Fashing, 2001b
C. vellerosus	Baobeng-Fiema, Ghana	59.1	23.7	14.6	2.6	Wong & Sicotte, 2007
C. satanus	Douala-Edea, Cameroon	60	23	4	14	McKey & Waterman, 1982
C. polykomos	Tai, Ivory Coast	33.9	34.9	25.9[a]	5.3	McGraw, 1998a
C. polykomos	Tiwai, Sierra Leone	55	30	11.5	2[b]	DaSilva, 1992
C. badius	Tai, Ivory Coast	29.9	29.1	34.7[a]	6.3	McGraw, 1998a
C. verus	Tai, Ivory Coast	35	26.5	31.8[a]	6.7	McGraw, 1998a

[a]= travel includes foraging; [b]= social behavior included in other activities

Energy economy is found in those species with high foliage intakes, such as the colobines (Kay and Davies, 1994). Researchers have attributed high levels of inactivity by *Colobus guereza* and *Colobus polykomos* to behavioral thermoregulation (Dasilva, 1992;

Fashing, 2001b), a pattern observed in this study as well. Delacour's langurs showed the common folivore midday rest period during the summer months (Clutton-Brock, 1977; Oates, 1977). During the summer, *Trachypithecus poliocephalus leucocephalus* stays obscured from view between 1130-1430 in either caves or vegetation (Li et al., 2003), with 4-5 hours of resting at midday (Huang et al., 2003). In the *T. p. leucocephalus* karst habitat of Guangxi Province, China, the bare rock heats up quickly (as the karst does at VLNR) and the langurs show thermoregulatory behaviors such as sunbathing in winter (Huang et al., 2003; Li and Rogers, 2005).

Several primate species spend time in sunning behavior (*Colobus guereza*: Oates, 1977; *T. p. leucocephalus*: Huang et al., 2003; *Lemur catta* (Jolly, 1966); and *Propithecus verreauxi*: Richard, 1978). As reported for *T. p. leucocephalus* (Huang et al., 2003), I observed that Delacour's langurs rested on bare rocks during the winter months, but unlike Huang et al. (2003), I did not score this behavior separately as sunbatheing. During summer, Delacour's langur groups spent time in rocky cave-like ledges, where young animals played and adults rested and groomed (Figure 23). These rocky areas created windtunnels and shaded rocks that were cooler than surrounding areas (personal observation). As further evidence that Delacour's langurs used thermoregulatory behaviors, they hunched over during rainstorms (Oates 1977; Fashing, 2001b) and stayed dry under rocks and in caves during rainstorms.

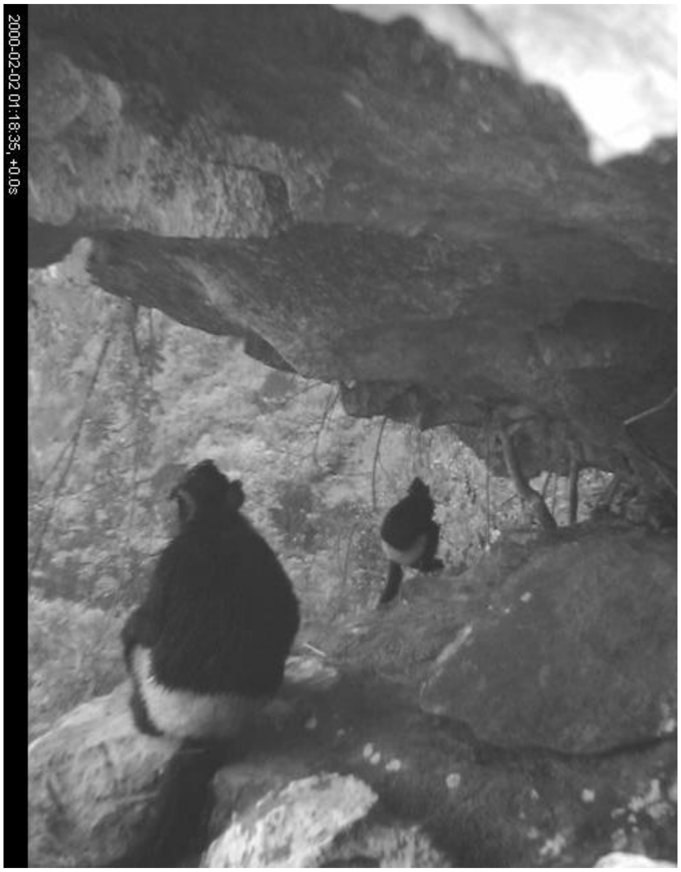

Figure 23: Rock shelters have shaded rocks and wind tunnels that stay cooler than surrounding habitat during the heat of summer days

Like Delacour's langurs in this study, *Trachypithecus poliocephalus leucocephalus* at Fusui Reserve, China showed no significant seasonal change in activity budget (Li and Rogers, 2004). For some Asian colobines, however, activity budgets change seasonally, a shift related to vegetation abundance and food quality. In Hubei and Shaanxi, China, *Rhinopithecus roxellana* spent more time traveling in summer and autumn, when food species richness and availability were greatest, and the least amount of time traveling in winter, when richness and availaibility dropped (Li, 2002). The high-altitude Nepalese

Semnopithecus entellus devotes a greater proportion of its activity budget to feeding as plant abundance decreases in fall and winter (Sayers and Norconk, 2008). At VLNR, chemical similarities of eaten leaves between seasons (Workman and Le Van Dung, 2009; Chapter 6), year-round availability of young leaves (Chapter 4), and a lack of increased seasonal travel or annual high frequency of time spent traveling (this chapter) indicates that langurs are not foraging extra during times of least abundant resources and that they are meeting their nutritional requirements. Alternatively, however, colobines may act passively during times of food scarcity and forage less (Oates, 1994), a strategy which must also be considered for these data at Van Long.

That Delacour's langurs are spending a large amount of their time resting, and that they are not engaged in excessive amounts of feeding or travel compared to other colobines may suggest that the habitat at VLNR is providing the langurs with what they need. Though based on activity budget data Delacour's langurs do not appear to be food stressed (a position championed by the year-round availability of young leaves), data on daily path length at VLNR across seasons and years would be necessary to clarify the situation. Future studies of activity budgets on this species should also include a fuller assessment of habitat, to elucidate how resource quality and distribution at VLNR affects activity patterns.

8. Positional Behavior

8.1 Introduction

Despite a very small amount of time spent locomoting, locomotion is important in colobine foraging not only because an animal must find and locate food, but because it must do so efficiently (Rose, 1979). Limestone langurs forage in environments with many exposed rocky substrates (*Trachypithecus poliocephalus leucocephalus*: Huang and Li, 2005; Li and Rogers, 2005; *T. poliocephalus, T. laotum hatinhensis, T. delacouri:* personal observation), yet there has been no quantitative study of the positional behavior of any of the rock-climbing, partly 'terrestrial' limestone langurs. Here, I report on the postural and locomotor behavior, support use, and related maintenance behaviors of Delacour's langurs. How terrestrial are Delacour's langurs? Is terrestrialism an accurate term to describe their use of rocky substrates?

I use these descriptive data to include Delacour's langurs in a broader locomotor issue: what is the the correlation between body size, diet, and locomotion in colobines? Is the positional behavior of this species- especially the degree of terrestrialism and leaping frequency- reflected in its morphology? Finally, I contribute these data to the recently reopened question of whether some Asian colobines are semibrachiators.

8.2 Methods

8.2.1 Positional Behavior of Delacour's Langurs

I observed the positional behavior of Delacour's langurs in Van Long Nature Reserve, Vietnam from June 2007-July 2008. I collected positional behavioral data in a similar manner to feeding and activity budget data collection (Workman, 2010; Chapter 5, 7). All data were collected from unhabituated langur groups living on Dong Quyen Mountain using the focal animal continuous sampling technique (Altman, 1974). Both the langur groups and the habitat have been described previously (Chapters 3, 5). During a focal animal follow, I recorded:

1. Time of day
2. Positional activity- locomotor or postural activity (Table 29). I used Hunt et al.'s (1996) list of 118 positional behaviors (49 postures and 69 motions) as possible positional behaviors.
3. Substrate- *tree* (recorded if the full weight of the focal langur was on any woody vegetation (tree or shrub) or *rock* (exposed rock or if the substrate was rock covered in climbing vegetation)
4. Related maintenance activity- *Feed, Travel, Rest, Social, Drink* (Table 6).

I recorded each change of posture or locomotion, even if the associated activity did not change. I used the focal animal continuous bout sampling method because this method maximizes the information gained from movement sequences and has been used previously in studies where animals were neither collared nor individually identified (Doran, 1993a, 1993b; Gebo and Chapman, 1995a). While instantaneous data collection may be more amenable to statistical testing, the time intervals used are frequently too short to be independent data points (Dagosto, 1994). Further, an advantage of locomotor bout data is that it captures rare events (such as leaping) that instantaneous sampling misses (Doran, 1992). A bout was defined as a change in positional behavior (Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995b). Each bout included a single behavior, bounded by a different posture or movement (see Fleagle, 1976; Fleagle and Mittermeier, 1980; Gebo, 1992). Postures used during rest typically last for longer periods of time, but each was still scored as a single bout (Gebo and Chapman, 1995b).

Another reason that bout data is preferable to instantaneous data is because the latter requires large sample sizes for analysis (Dagosto, 1994). Gebo and Chapman (1995b) note that 6,500 bouts are needed to characterize positional behavior because only small changes seem to occur in the frequencies of positional behavior after 3,000 bouts. Following the methods of Gebo and Chapman (1995a), I collected nearly 14,000 bouts of positional behavior of which 7,500 were locomotor bouts (Table 28), exceeding Gebo and Chapman’s (1995a) suggested minimum 6,500 bouts needed to represent a species. Following Walker (1998), positional behaviors were collapsed into major postural and locomotor modes that are biomechanically similar (Table 29).

Table 28: ***Trachypithecus delacouri*** **and the nature of the sampling of locomotor bouts collected (after Gebo and Chapman, 1995a)**

Trachypithecus delacouri	
Body weight (g)*	
Males	8,600
Females	7,800
Male/Female ratio	1.1
Mean weight (g)	8,200
Total bouts	13,916
Locomotor bouts	7,522
Postural bouts	6,394
Contact hours	476

*Nadler et al., 2002

Table 29: Definitions of positional activities (after Gebo and Chapman, 1995; 2000)

Locomotion

Quad= quadrupedalism: all four limbs move in a regular pattern above a support or on the ground; includes walking, running, bounding, and galloping.

Climb= movements which generally require greater mobility in the limbs; a movement up or down a vertical or steeply inclined support or rock or through intertwined and small supports; all four limbs move in an irregular pattern with abducted arms and knees and with variable hand and foot positions.

Leap= a movement in which the hindlimbs propel the animal across a gap; includes quadrupedal standing then leaping or pumping the body up and down before leaping, vertical clinging and leaping, and quadrupedal running and leaping. Droppping down from a substrate was not scored as a leap.

Other= includes *bipedal walk* and *bipedal hop*, in which only the hind feet are used to travel short distances; suspensory movements, in which either one (*unimanual swing*) or both (*bimanual swing*) forelimbs are used to progress the body below a support; droppping from suspensory postures, in which the animal drops while hanging from one (*unimanual drop*) or both (*bimanual drop*) forelimbs; *bimanual pullup*, in which the hands grasp a support and are used to pull the rest of the body up to a support from below; *quadrupedal drop*, in which the animal drops to a lower substrate without leaping; *scooting*, in which the hindquarters are slid along a substrate with the hindlimbs; *poleslide*, in which an animal slides vertically down a bamboo pole.

Postures

Sit= animal supports weight on its haunches; feet may or may not be in contact with the support, above or below the body; can sit with feet in toward the midline of the body or spread outward;

Stand= animal stands on all four limbs

Recline= animal lies on its belly, side, or back

Other= includes, *vertical clinging*: animal clings to vertical support without sitting; suspension, in which an animal hangs underneath a support by all four limbs (*quadrupedal suspend*), both forelimbs (*bimanual suspend*- ususally with bent elbows), one forelimb (*unimanual suspend*), or hindfeet (*hindlimb suspend*); *bipedal stand*: animal stands on hindfeet, usually with the heel elevated above the support.

8.2.2 Statistical Analyses

Positional behavior studies have been plagued by statistical analysis problems created by interdependent data points and data collected on a small (often unknown) number of individuals (Dagosto, 1994). Studies of positional behavior in which duration of time is the unit of measurement are not conducive to statistical analyses, because units of time are not independent measurements and the locomotor data collected at one instant is dependent on the behavior performed immediately prior (Cant, 1987, 1988; Dagosto, 1994; Gebo and Chapman, 1995a, 1995b). The locomotor and postural data presented here are therefore mostly descriptive frequencies, but I also follow previous researchers in using a Chi Square to test numbers of bouts between age and sex classes (Cant, 1988). To test relationships between morphology and locomotion, total frequency (%) of leaping by Delacour's langurs against a) body mass and b) intermembral index as well as c) body mass against intermembral index is compared to other Cercopithecinae for which the same data are known using a Spearman Correlation in XLSTAT 2009. Significance was set at P=0.05.

8.3 Results

8.3.1 Positional Behavior

Delacour's langurs exhibited 23 total locomotions and 16 postures during the study period. Frequencies of overall locomotion were collapsed into four main categories of quadrupedalism, climbing, leaping, and other locomotor behaviors. Delacour's langurs spend 2/3 of their locomotor time quadrupedally, more than double that of climbing, the next most frequent locomotion; however, leaping is almost as rare as the category of "other" behaviors that includes suspensory movements and bipedalism (Figures 24, 25). Sitting (95%) dominated postural behaviors with only 3% and 2% of postural bouts spent standing and reclining, respectively (Figure 26). Other postures (including bimanual, unimanual, and quadrumanous suspend positions) accounted for less than 1% of postural bouts.

Figure 24: Quadrupedalism on rocks is Delacour's langurs' most frequent locomotion

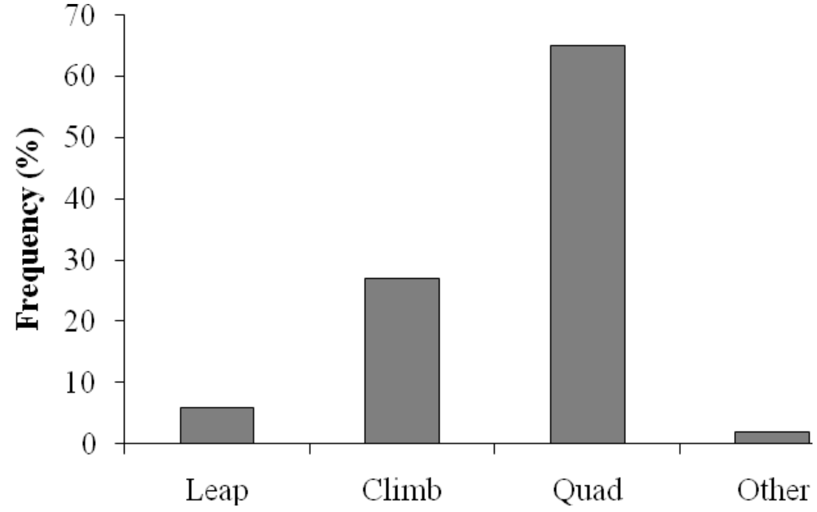

Figure 25: Locomotor behavior of Delacour's langurs

Figure 26: Postural behaviors are dominated by sitting

8.3.2 How Terrestrial are Delacour's Langurs?

Delacour's langurs spent more than 80% of their locomotor time on rocks (Figure 27). Overall, trees were not used as frequently as rocks in the habitat, yet there are differences in the time spent in maintenance behaviors on rocks versus trees. Nearly 90% of socializing, traveling, and resting was performed on rocks (Figure 27). The VLNR karst habitat has many sharp, razor-like points and steep angles, but langur groups would often rest and socialize on larger, relatively flatter – but still pointed- rocky outcrops. As reported for gray langurs on Ceylon (Ripley, 1967), quadrupedal standing for prolonged social behaviors such as grooming, mounting, and presenting occurred on sturdy substrates (ie rocks at Van Long, large branches at Ceylon).

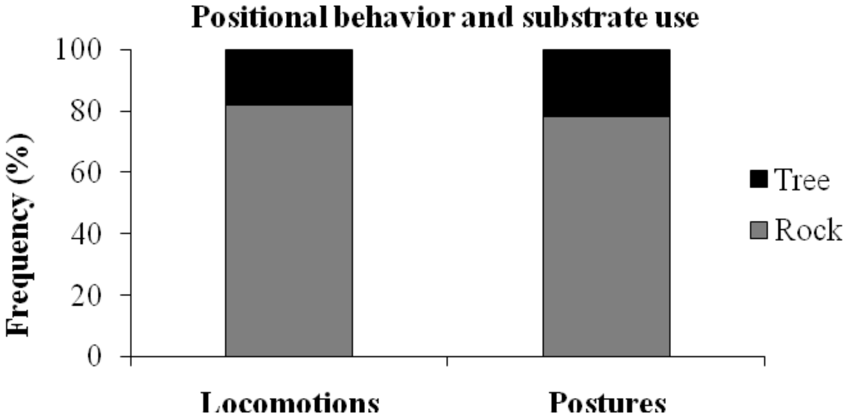

Figure 27: Frequency of positional behavior and support type

Unlike social, travel, and rest behaviors, feeding time was split evenly between rocks (48%) and trees (52%) (Figure 28). When they fed on rocks, langurs would sit level with a tree and pull the leaves directly to their mouth. Of their annual diet, 53% of the species that langurs ate were climbers, most of which grew over rocks, and were therefore eaten by sitting on rocks (Figure 29). Though some of these surfaces were sharp, langurs were often protected from their rocky points by sitting on the climbers that covered them. Further, langurs would sit on sharper or more angled surfaces for feeding than they used for resting or social behaviors.

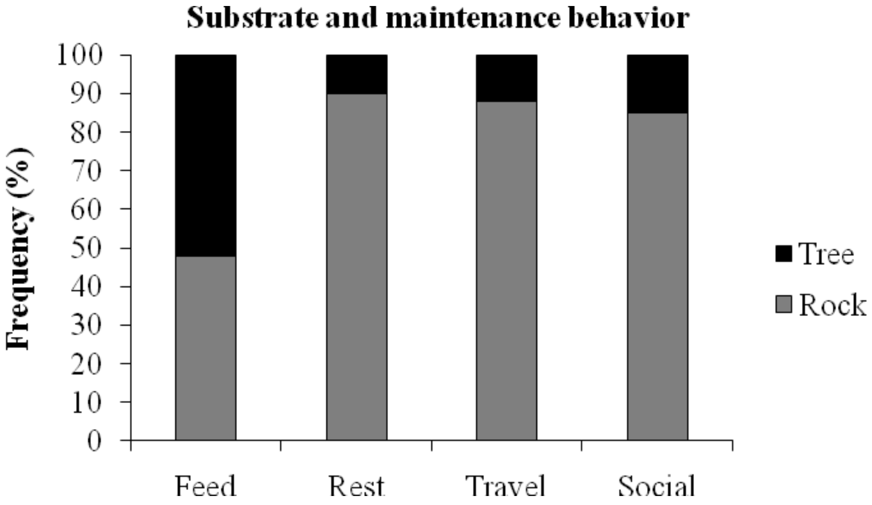

Figure 28: Support type and maintenance behaviors by Delacour's langurs at Van Long Nature Reserve, June 2007-July 2008

Figure 29: Langurs frequently sit on rocks to feed, pulling climbers (here: Ipomeae bonii) towards themselves

Locomotion varied by substrate (Table 32). Quadrupedalism was the most frequently performed locomotion on both rocks and trees, yet there are interesting differences in the frequency of climbing and leaping between substrates (Figure 30). Langurs spent nearly double the amount of time climbing on rocks (28%: Figure 31) than on trees (15%) yet leapt three times more frequently on trees (13%) than on rocks (4%). Further, when leaping between support types, langurs more frequently used trees as a landing substrate than rocks (38% vs. 23%). The longer, "daredevil" leaps (Ripley, 1967:161) performed by Delacour's langurs usually involved moving from a sturdy support above (rock) to a flexible support(s) below, often a tangle of tree branches. This substrate progression was frequently used by subadult langurs during social play. One day, I observed three subadults of St7 throw themselves from a rock into trees below four times successively. The subadults did not appear to simply be chasing one another, but rather to be leaping repeatedly from the rock into the trees as children would from a diving board into water. Langurs used quadrupedalism least frequently moving from rocks to trees, while all *other* locomotor behaviors occurred most frequently on trees.

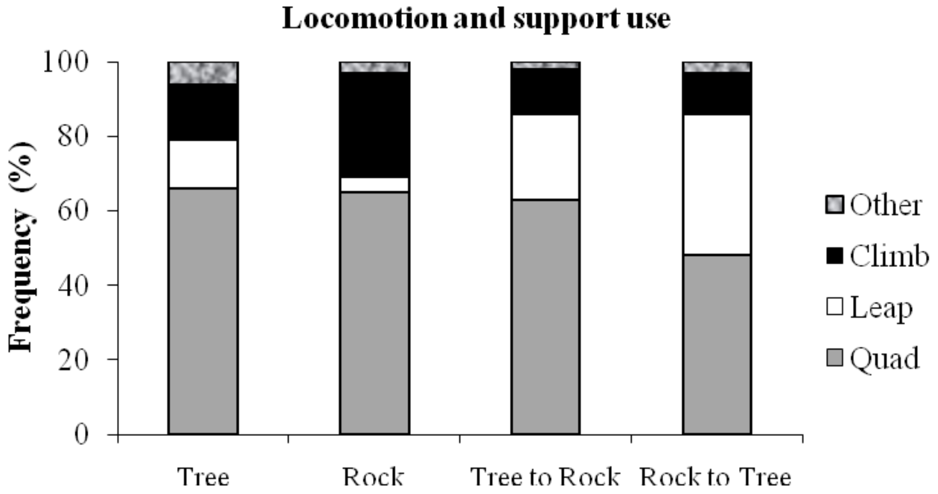

Figure 30: Frequency of locomotor behaviors on different substrates by Delacour's langurs at Van Long Nature Reserve, June 2007-July 2008

Figure 31: Rocks are used more than trees for travel

8.3.3 Age and Sex Differences in Positional Behavior

Female Delacour's langurs exhibited more total locomotor behaviors (23) than the other age/sex groups, but the difference was not significant ($x^2 = 2.510$, df = 3, P = 0.47, Table 30). The age and sex breakdown of locomotor behaviors mirrors that of the overall frequencies: quadrupedalism was most frequently used by all groups (Figure 32). Adults and subadults used quadrupedal movements more frequently than climbing in locomotion during travel, with leaping accounting for a much smaller proportion of locomotion during feeding (Table 31). During travel, females with infants leapt the least and subadults leapt the most. Subadults were the only group to use leaping during social (play) behavior. Climbing was used less frequently while feeding than during travel. Leaps were infrequent for all adult groups during feeding, but subadults employed leaping more frequently (31%). During rest, all age and sex groups used sitting postures nearly 100% of the time (Table 31). Sitting postures were used most frequently while feeding, yet there was slightly more variation of postures during feeding than during the other maintenance behaviors.

Table 30: Number of observed postural and locomotor behaviors by age/sex class

	Male	Female	Female with infant	Subadult
Locomotions	14	23	16	14
Postures	14	16	12	14

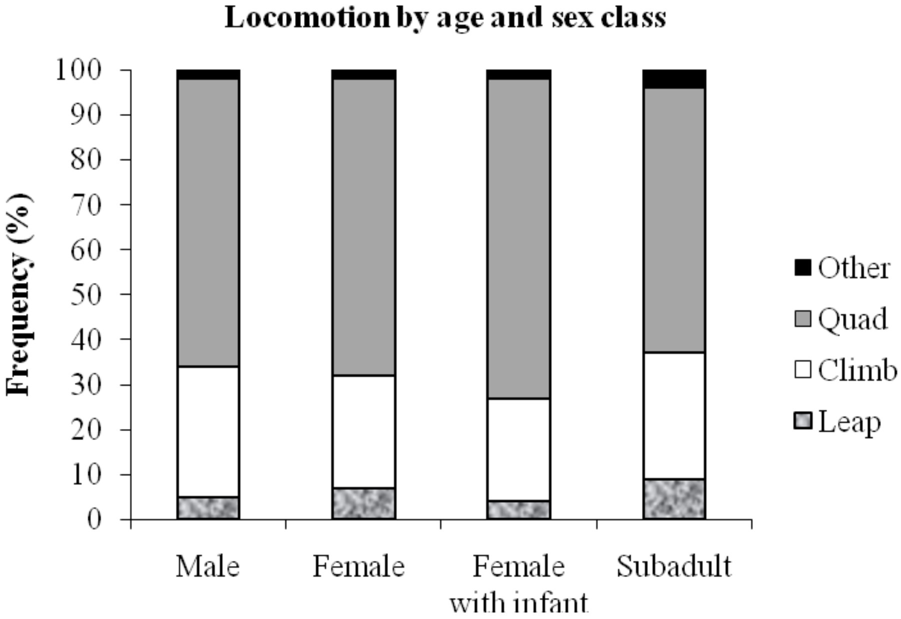

Figure 32: Locomotor frequencies by age/sex class

Table 31: Locomotor and postural frequencies by activity for age/sex classes (after Gebo and Chapman, 1995a)

	Locomotor Frequencies				
	N	**Quad**	**Leap**	**Climb**	**Other**
Travel					
Males	2707	65%	6%	28%	1%
Females	3030	63%	9%	27%	1%
Females with baby	754	70%	4%	24%	2%
Subadults	557	57%	11%	26%	6%
Feeding					
Males	86	77%	10%	12%	1%
Females	239	79%	8%	8%	5%
Females with baby	38	92%	0%	8%	0
Subadults	13	54%	31%	15%	0
Social					
Males	16	100%	0	0	0
Females	15	87%	0	0	13%
Females with baby	0	0	0	0	0
Subadults	67	28%	40%	28%	4%
	Postural Frequencies				
	N	Sit	Stand	Recline	Other
Resting					
Males	1702	98%	<1%	1%	<1%
Females	1708	98%	<1%	1%	<1%
Females with baby	410	98%	0	1%	<1%
Subadults	303	99%	1%	0	0
Feeding					
Males	529	95%	5%	0	<1%
Females	843	91%	8%	0	<1%
Females with baby	172	94%	6%	0	0
Subadults	156	88%	11%	0	<1%
Social					
Males	123	71%	22%	7%	0
Females	317	72%	21%	6%	<1%
Females with baby	79	79%	16%	5%	0
Subadults	36	89%	0	11%	0

Table 32: Locomotor behaviors and support type by age/sex class

	N	Quad	Leap	Climb	Other
TREE					
Males	218	118	34	49	17
Females	497	363	45	57	32
Female with infant	60	40	11	8	1
Subadults	42	14	14	10	4
Frequency	817	66%	13%	15%	6%
ROCK					
Males	2,326	1,564	12	688	62
Females	2,462	1,500	188	695	79
Female with infant	630	465	14	138	13
Subadults	550	363	16	139	32
Frequency	5,968	65%	4%	28%	3%
TREE to ROCK					
Males	102	57	26	19	0
Females	145	101	27	11	6
Female with infant	40	29	6	5	0
Subadults	18	4	12	1	1
Frequency	305	63%	23%	12%	2%
ROCK to TREE					
Males	163	72	65	23	3
Females	178	96	61	13	8
Females with baby	38	21	13	4	0
Subadults	33	10	16	6	1
Frequency	412	48%	38%	11%	3%

8.3.4 Suspensory Behaviors

Delacour's langurs spent a small percent of time in *other* locomotor (2%) and postural (<1%) behaviors. Of the locomotor behaviors that did not fall into quadrupedalism, climbing, or leaping, only 0.8% (60 bouts) were suspensory (Table 33). Delacour's used *bimanual* (8 bouts) and *unimanual swing* (42), *bimanual* (19) and *unimanual drop* (4), *and bimanual pullup* (9). Of suspensory locomotions, 37% were performed on arboreal supports. Suspensory locomotion occurred overwhelmingly during travel (94%) with only 5% during feeding, and 1% during subadult social play. Delacour's langurs expressed 13 suspensory postures during the study period: *quadrupedal* (2), *bimanual* (4), *unimanual* (3), and *hindlimb suspend* (4). All suspensory postures were performed on trees, 87% during feeding by adults and 13% during social play behavior by subadults.

Table 33: Suspensory postural and locomotor behaviors recorded for Delacour's langurs at Van Long Nature Reserve from June 2007-July 2008

Total Locomotor Bouts	Suspensory Locomotions	% of Locomotion
7,522	81	1
Total Postural Bouts	**Suspensory Postures**	**% of Postures**
6,394	13	0.2

8.4 Discussion

8.4.1 Positional Behavior

Delacour's langurs are predominantly quadrupedal colobines. Of greatest interest in this study were the two anomalous results which set Delacour's langurs apart from other colobines on which positional behavior data have been collected. First, Delacour's langurs were not highly arboreal in this habitat: nearly 80% of locomotor and postural behaviors were performed on rocks. Second, Delacour's langurs were not frequent leapers: only 6% of their overall locomotion was leaping.

8.4.1.1 Postures, Substrate Use, and Sex Differences

Despite the attention given to differences in major locomotor modes, the majority of positional behavior time is devoted to postural activities such as sitting, standing, and reclining during feeding, resting, and socializing activities (Rose, 1973; Doran, 1993b; McGraw, 1998a). That Delacour's predominantly used sitting postures was therefore expected. The dominance of sitting in overall posture frequency was seen by three colobus species of the Tai Forest, Ivory Coast who employed sitting postures most frequently during feeding, resting, and socializing (McGraw, 1998a). Whereas platyrrhines rest and sleep in reclining postures, catarrhines employ high amounts of sitting during rest, a posture aided by ischial callosities (Napier, 1967). Sitting on ischial callosities would be especially important at VLNR, where the majority of time is spent on rocks rather than trees, yet where the razor-like rocky habitat makes reclining and lying less comfortable or possible.

Several studies have shown that primates use larger supports during travel than during foraging (Surinam monkeys: Fleagle and Mittermeier, 1980; *Macaca fascicularis*: Cant, 1988; Kibale cercopithecids: Gebo and Chapman, 1995a). Using the layer or path of canopy that contains sturdy supports is important for large-bodied colobines, because despite appearing so, the canopy is often not continuous. Even if overlapping twigs create the illusion of connectedness, large-bodied colobines are unable to walk out their weight to the termination of small twigs (McGraw, 1998b). McGraw's (1998b) expectation that sturdier, bigger supports should be used during travel with smaller, more flexible supports used during foraging and feeding can logically be applied to rock versus tree use at VLNR. Trees capable of supporting the weight of Delacour's langurs are less available than rocks. Chimpanzees in Tai Forest, Ivory Coast spend more time traveling terrestrially and feeding arboreally (Doran, 1993b), a difference also seen at VLNR, where langurs travel more frequently on rocks. Future studies at VLNR need to quantify the availability of rocks versus trees in the habitat to determine if langurs prefer rocks as a substrate or if they are most available.

No differences between male and female Delacour's langurs were expected given the lack of statistical differences between male and female red colobus monkeys in Kibale National Park (Gebo and Chapman, 1995b) as well as the small behavioral differences even for species that are highly sexually dimorphic in body size (*Pongo pygmaeus*: Cant, 1987; *Gorilla gorilla gorilla*: Remis, 1998). Doran (1993a, 1993b) found no overall sex differences in positional behavior for *Pan troglodytes verus*, but found differences in the type of locomotion used during feeding and travel as well as substrates used during these activities. Female chimpanzees employ arboreal quadrupedalism more than males, who scramble and climb more, due to the lack of large enough substrates to support them during arboreal quadrupedalism (Doran, 1993a). In addition to minimal body size dimorphism, the fact that males and females do not differ much in their locomotion at Van Long may be attributed to the treacherous habitat. Instead of individuals finding their own path across and especially up and down steep rock faces, individuals trail one another during travel. This follow-the-leader style movement has also been reported for *Trachypithecus francoisi* (Zhou et al., 2009b). The consequences of such a style are safety for the followers and a lack of diversity in locomotor positions.

8.4.1.2 The Significance of Cliff-Climbing by Limestone Langurs

Trachypithecus poliocephalus leucocephalus spends about 70% of its locomotor time on rocks and cliffs, with 25% on cliffs and about half of all locomotion on rocks (Huang and Li, 2005). In this study, I did not distinguish between the time Delacour's langurs spent on rocky cliffs versus non-cliff rocky substrates, but the overall percentage of time spent on rocks is similar (80% for Delacour's langurs). Behavioral flexibility allows limestone-living *Trachypithecus* to adapt to a range of habitats, and to access necessary caves and resources on karst cliffs. The location of sleeping caves and sleeping rocks indicates that limestone langurs have the ability and willingness to scale precipitous substrates to avoid danger or weather. Conversely, a primate's willingness to come to the ground is essential in patchy habitats (Oates, 1977). While colobines typically do not descend to the ground to feed or drink, those living in fragmented habitats do frequently descend to cross deforested patches (Struhsaker and Leland, 1987; Kirkpatrick, 2007). Compared to colobines, terrestrial locomotion allows cercopithecines the flexibility to exploit a range of habitats (Fleagle, 1999). In Senegal, terrestrial locomotion by *Procolobus badius temmincki* during the past 30 years has been adaptive in degraded habitats which lack arboreal pathways (Galat-Luong and Galat, 2005). Similarly, the incorporation of cliff-climbing locomotion by several of the Asian species might reflect a wider adaptive capacity than was once known. The broader impact of cliff-climbing by the limestone langur species might not only be in how it influences their use of habitat, but in the adaptive value it has on avoiding predators and foraging (Grand, 1978).

Studies of tail use might provide clues to locomotor adaptation. In an analysis of the arboreal balancing mechanisms of five Old World monkey species, Larson and Stern (2006) found that when travelling above ground on a 15cm support, the largest and most terrestrial species (*Papio anubis* and *Erythrocebus patas*) used a balancing tail-whip behavior more than did the smaller, more arboreal species. The authors suggest that the former are less adept at arboreal locomotion and therefore use the tail as a balancing mechanism when above ground. Stevens' et al. (2006) recently compared the tail posture of two *Pygathrix* species with *Trachypithecus delacouri* and *T. laotum hatinhensis*. They found that, when walking on two-inch diameter horizontal supports in captivity, *Trachypithecus delacouri* arch the tail in a downward concave posture. By contrast, *Pygathrix* drops the tail, while *Trachypithecus laotum hatinhensis* displays the most variety in tail posture, frequently raising the tail in a concave-upwards arc with the tail extending over the back. The authors suggest that these differences in tail posture might reflect the use of different wild substrates, although the two *Trachypithecus* species share similar habitat types. It is interesting that the two *Trachypithecus* species are less arboreal than *Pygathrix* in the wild, perhaps necessitating a tail-whip mechanism similar to that of the patas monkey and baboon.

Cliff-climbing is something altogether different from either terrestrial or arboreal locomotion. The degree of danger involved in scaling rocky cliffs and climbing across sheer rock faces is quite separate from that of walking across a savannah or even irregular ground. The so-called terrestrialism employed by the limestone langurs is not terestrialism at all. The 'terrestrial' surfaces limestone langurs scale are vertical and the grip and tension needed to stay in contact with the substrate competes with the forces of gravity. Simply put, most every terrestrial animal cannot fall off their substrate. For these reasons, neither arboreal nor terrestrial will suffice in describing the locomotor profile of langurs in a limestone habitat. The term 'cliff-climbing' should be used to indicate the substrate, the verticality, and the danger of this type of locomotion.

8.4.1.3 Are Delacour's Langurs Semibrachiators?

Despite seeming misappropriation of the term since the 1970s, the semibrachiator label is now appropriately applied to some Asian colobines. Red- and grey-shanked douc langurs (*Pygathrix sp*.) employ suspensory behaviors in numbers equal to or greater than that of the New World suspensory spider monkeys (*Ateles sp)* (Byron and Covert, 2004; Wright et al., 2008a). When *Trachypithecus delacouri* was studied in an identical captive setting as *Pygathrix*, however, the former did not show a propensity for suspensory locomotions (Byron and Covert, 2004; Workman and Covert, 2005). According to this study, their positional behavior in the wild is no different. Like many African and Asian colobines (Ripley, 1967; Fleagle, 1977a, b, 1978; Rose, 1978; Gebo and Chapman, 1995a; McGraw, 1998b), suspensory postures and locomotions are a tiny fraction of the Delacour's langur mostly quadrupedal positional behavior in the wild, and therefore the term semibrachiator should not be applied to them.

8.4.2 Why are Delacour's langurs infrequent leapers?

Compared to African and Asian cercopithecids, it is conspicuous how little Delacour's langurs leap (Table 34). Colobines in general are well-known for their tremendous leaping abilities (Struhsaker and Leyland, 1987), yet *Presbytis melalophos* leaps ten times more, *P. obscura* and *Colobus guereza* six times more, and *Procolobus badius* five times more than does the Delacour's langur (Table 34). The lack of leaping in the Delacour's langur repertoire is not due to an inability for such movements. During the course of this study, male, female, and subadult Delacour's langurs were observed performing leaps of great distance, mostly during travel (Figure 33). In Kibale and Tai Forests, climbing is more frequent during foraging and leaping is more common during travel (Gebo and Chapman, 1995a; McGraw, 1998b). Three possible explanations for the small degree of leaping by Delacour's langurs are 1) substrate availability in a karst habitat 2) the amount of foliage in their diet and 3) body size.

Figure 33: Though they rarely do, Delacour's langurs are capable of magnificent leaps

Table 34: African and Asian cercopithecids (adapted from Gebo and Chapman, 1995a)

	Body weight (g)	Leaping (%)	Intermembral index
Colobines			
African			
Procolobus badius[a]	8,245	30	87
P. verus	4,500[b]	20.4[c]	80[b]
Colobus guereza[a]	9,070	44	79
C. polykomos	9,100[b]	14.5[c]	78[b]
Asian			
Presbytis melalophos[a]	6,648	67.5	78
P. obscura[a]	6,810	40.2	83
Trachypithecus delacouri	8,200[d]	6[f]	76.5[e]
Cercopithecines			
African[a]			
Chlorocebus aethiops	4,365	10	83
Cercocebus ascanius	3,585	25	79
C. mitis	4,750	18	82
C. albigena	7,690	21	78
Asian[a]			
Macaca fascicularis	4,030	11	93

[a]Gebo and Chapman, 1995a; [b]Fleagle, 1999 (*P. verus* and *C. polykomos* determined by taking average of male and female weights); [c]Garber, 2007; [d]Nadler et al., 2002; [e]Bert Covert, personal communication; [f]this study

8.4.2.1 Leaping and Substrate Availability

Locomotion and support type at VLNR are difficult to compare to other non-karst colobine and primate studies, because Delacour's langurs spend 80% of their locomotor time on rocks – a substrate not considered in previous positional behavior studies- and tree sizes were not quantified in this study. While many tropical habitats have multiple levels of forest (a low shrub layer, an understorey, middle and upper canopy layers: Whitmore, 1998), Van Long's vegetation is mostly restricted to the first layer of shrubs under eight meters. Because there is no usable understory or middle canopy, no relationship between body size and forest layer can be determined. Ripley (1967) described medium-sized trees with large, low-branching limbs as a common component of langur habitat, but such trees are not largely available at VLNR. Limestone karst is a unique substrate. Karst cannot be classified as strictly terrestrial because this environment does not offer a stable, uniform substrate of continuous pathways (Garber, 2007), but rather a distinctly challenging, sometimes dangerous, inconsistent support that demands cautious climbing and quadrupedal progression.

That colobines seem to crash into a more general area when they leap compared to more precise leaping by guenons (Struhsaker, 1975) is supported by observations at VLNR. During the study period, the longest and most spectacular leaps terminated in trees, never on rocks, which are sharp. Leaps did occur more often during travel than feeding, a pattern observed in other primates (Fleagle and Mittermeier, 1980). The leaping specializations of *Presbytis melalophos* and *P. rubicunda* are adaptive in efficiently locomoting through a discontinuous forest understory (Fleagle, 1978; Davies, 1984), yet despite being sharp and non-uniform, rocks at VLNR are mostly continuous. Van Long has no understory and there is not a discontinuity of substrates, but rather a type of substrate (rock) that is better negotiated with locomotions that keep the animal close to the support. Simply put, it may be too dangerous to leap frequently in this habitat.

8.4.2.2 Leaping and Leaf Eating

Digesting leaves is relatively inefficient, and therefore colobines must spend a sizeable portion of their day inactive and digesting (Eisenberg, 1978; Fleagle, 1984). Due to their folivorous diets, colobines sit more than cercopithecines because leaves tend be more abundant and can be exhausted without getting up (McGraw, 1998a). In addition, more time is needed for digestion of fibrous material (Kay and Davies, 1994; Oates 1994). Delacour's langurs are one of the most folivorous colobines for which there are data (Workman, 2010; Chapter 5), yet they show the lowest degree of leaping (Table 34). Is there a relationship between this high degree of folivory and low amount of leaping? The answer is unclear. *Colobus guereza*, the most folivorous of the African colobines (87.5% leafy diet at Kibale, Uganda: Harris and Chapman, 2007) is also one of the most frequent leapers (44% at Kibale: Gebo and Chapman, 1995a). Yet in a comparison between Malaysian *Presbytis obscura* and *P. melalophos*, Fleagle (1978) found that the two species differed in their frequency of leaping and the percentage of foliage in their diets. The less folivorous *Prebytis melalophos* leapt more and used quadrupedal locomotion less compared to the more folivorous *P. obscura*. McGraw and Zuberbuhler (2008) report no simple associations between body size and major diet categories in Tai Forest monkeys, and conclude that diet is not an accurate predictor of any single behavior, such as leaping.

McGraw (1998b) questioned how efficient a strategy of relative inactivity coupled with leaping is for folivorous colobines. He suggests that colobines may maximize their foraging efficiency- compared to that of cercopithecines- by minimizing their energy expenditure by leaping during feeding (McGraw 1998b). This strategy is unlikely to apply to Delacour's langurs, which leap most frequently (when they leap at all) during travel, not feeding. Further, teasing out a correlation between degree of leaping and degree of folivory is complicated, because there is a strong influence of body size on degree of folivory (McNab, 1978; Kay, 1984; Milton, 1993). By slowing gut passage time and allowing time for gut microbes to ferment the cell walls' cellulose and hemicellulose, larger folivores can process more fibrous plant foods (Milton, 1984), but arboreal colobines are limited by locomotor and safety (falling) costs in the amount to which they can expand somatic growth.

8.4.2.3 Leaping and Body Size

Cant (1992) offered a framework to understand the adaptive (he used *aptive*, following Gould and Vrba, 1982) relationship between primate body size and positional behavior, in which he advocated questioning and understanding how different taxa use their morphology and behavior to solve ecological problems. At VLNR, the influence of body size is hardly a consideration the way that it is for arboreal monkeys which must assess the ability of terminal branches to support their weight, but closer to that of terrestrial animals freed of body weight considerations (Fleagle, 1985).

Differences in primate positional behaviors are more likely related to dietary and morphological adaptations than they are to body mass (Garber, 2007), yet several authors have studied the relationship between body size and locomotion. Body size differences across the order Primates have led to expectations of dramatically different locomotor styles, and yet Fleagle and Mittermeier (1980) provided data from sympatric Surinam monkeys that did not clearly support body size as wholly predictive of locomotion. *Pithecia pithecia* leapt more and *Saguinus midas* leapt less than expected based on body size (Fleagle and Mittermeier, 1980). Building on platyrrhine data from Fleagle and Mittermeier (1980), McGraw (1998b) predicted that larger monkeys in Tai Forest, Ivory Coast would show decreased frequency of leaping and increased amounts of climbing compared to smaller Tai monkeys. However, among the six cercopithecid species that he studied, the largest bodied monkeys (colobines) leapt more than the smaller cercopithecines, but smaller colobines leapt more than larger colobines while larger colobines climbed more than smaller colobines (McGraw, 1988b). As body mass increased, so did frequency of leaping. Studies on five sympatric cercopithecoid species in Kibale, Uganda also did not support body size as a predictor of locomotion (Gebo and Chapman, 1995a). Garber (2007) stated that body size is not a strong predictor of positional behavior, and data from African and Asian cercopithecids have supported this statement.

Gebo and Chapman (1995a) compared quadrupedal African (*Procolobus badius*, *Colobus guereza*, *Chlorocebus aethiops, Cercopithecus ascanius, C. mitis*, and *C. albigena*) and Asian (*Presbytis melalophos*, *P. obscura*, and *Macaca fascicularis*) cercopithecids and found that the leaping frequencies of these taxa are not strongly affected by body size or intermembral index (Table 34). When *Trachypithecus delacouri* is added to the analysis, the significance of the results does not change. Body size is not highly correlated with leaping frequency (Figure 34), nor is the correlation coefficient significantly different from zero (r= 0.274, P=0.436). In fact, adding *T. delacouri* to the analysis makes the relationship between body size and leaping even less significant (r= 0.534, P=0.138 without *T. delacouri*), because of its infrequent leaping. The exceptionally high frequency of leaping by large-bodied guerezas (9kg, 44%) would seem to highlight or potentially unfairly obscure the small amount that Delacour's langurs leap, but Figure 34 also shows that even *Colobus badius*, slightly larger than Delacour's langurs (8.2 vs 8kg) leaps five times more than the Delacour's langur (30 vs 6%). Delacour's langurs leap less than equally large - and larger - colobines.

Including *T. delacouri* in the analyses did little to alter the correlations between intermembral index and body size (r = -0.325, P=0.361; Figure 35) and intermembral index and leaping frequency (r = -0.055, P=0.891; Figure 36). Longer forelimbs create more stability when traveling on the ground (Chivers, 1991), so the rock-traveling Delacour's langur might be expected to have longer forelimbs if this use of rocky substrates is not recent. In fact, Delacour's langurs have the lowest intermembral index (76.5) compared to these other cercopithecids. In his seminal paper, Prost (1965) distinguished between locomotor *habit* (preference) and *totipotentiality (*physical capability), saying that habits are important only where two taxa have the same capacity, or totipotentiality, to perform. For example, langurs and sharks do not have different habits, they have different totipotentiality. Conversely, Delacour's langurs and colobines that leap a lot are showing different habits. Having relatively long hindlimbs indicates that Delacour's langurs are morphologically capable of powerful leaping like other colobines. This behavioral totipotentiality, however, is now habitually underutilized in the rocky limestone karst habitat (Prost, 1965). This incongruence between morphology and behavior may be strong evidence that Delacour's langurs are not evolutionarily adapted for limestone karst.

Within the colobinae there is tremendous diversity of intermembral index which does not equate cleanly with observed locomotor patterns. The terrestrial behavior observed in *Rhinopithecus* (Kirkpatrick and Long, 1994) and limestone members of *Trachypithecus* is not necessarily revealed in their intermembral indices, although *Trachypithecus* shows a lower IMI compared to the more suspensory *Pygathrix, Nasalis,* and *Rhinopithecus* (Byron and Covert, 2004; Bert Covert, personal comunication). Colobines typically have longer hindlimbs as a group (IMI: 76-87) than the more terrestrial cercopithecines (*Macaca* IMI: 90-100; *Papio*: 100; *Erythrocebus patas* 92;

Chlorocebus aethiops 83; *Cercocebus agilis* 84) (Napier and Napier, 1985; Fleagle, 1999) and *T. delacouri* adheres to this pattern.

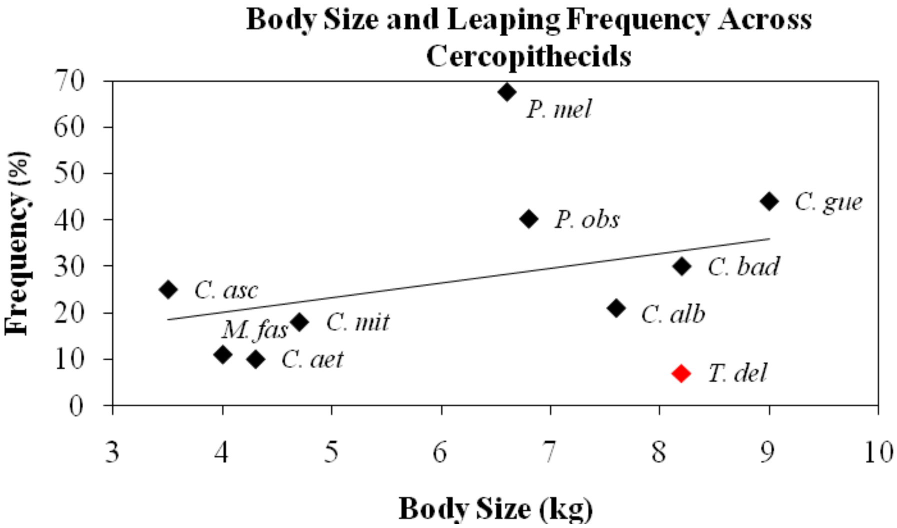

Figure 34: Body size and leaping frequency during travel (amended from Gebo and Chapman, 1995a to include this study (in red)). Data labels are first three letters of each species name. Species values listed in Table 34.

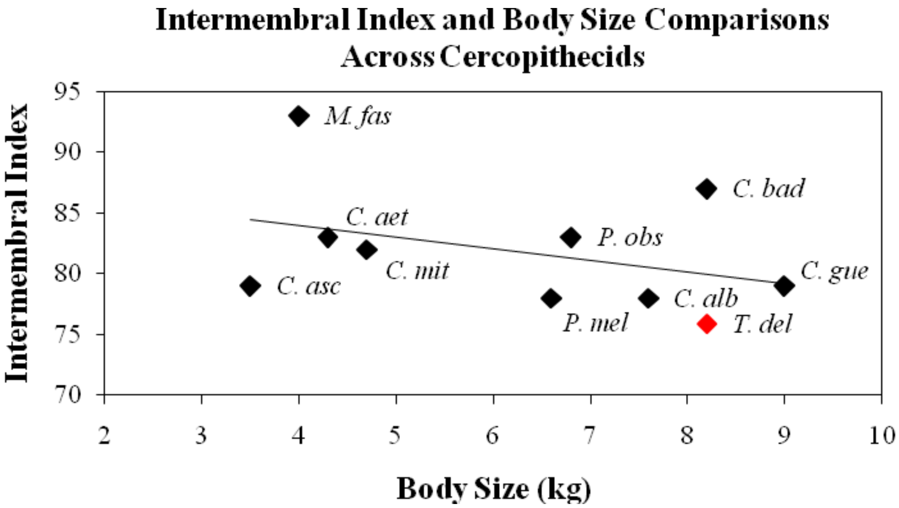

Figure 35: Comparison of intermembral index and body size across cercopithecids (amended from Gebo and Chapman, 1995a to include this study (in red)). Data labels are first three letters of each species name. Species values listed in Table 34.

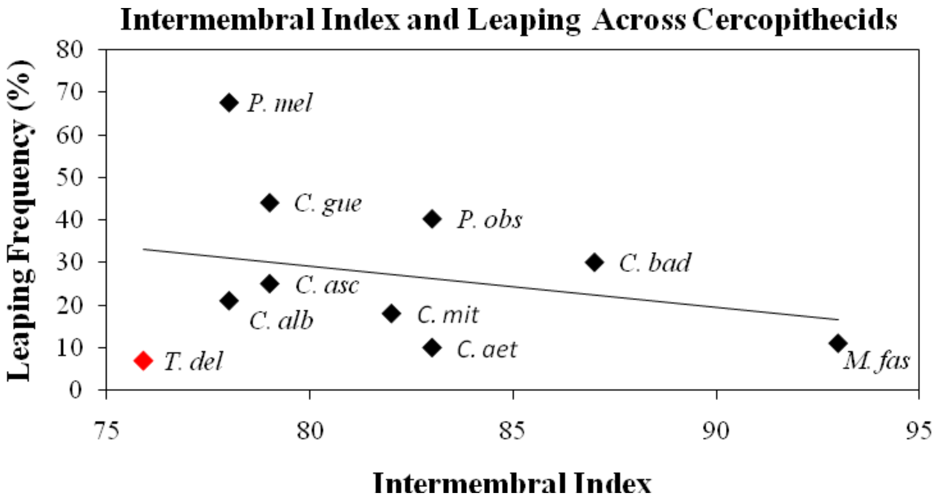

Figure 36: Intermembral index and leaping frequency during travel (amended from Gebo and Chapman, 1995a to include this study (in red)). Data labels are first three letters of each species name. Species values listed in Table 34.

In conclusion, Delacour's langurs are not a typical arboreal quadrupedal colobine. They leap and use trees far less than other colobines. Delacour's langurs spend the majority of their locomotor and postural time on rocky substrates, a novel support type in the colobine positional behavior literature. In this sense, Delacour's langurs corroborate and augment the existing data that Asian colobines are unexpected and highly interesting in their positional behavior. They are cliff-climbers.

Unknown at this time, however, is to what degree these differences in substrate type and leaping frequency are evolved species-specific - perhaps radiation-specific - tendencies of limestone langurs, and to what degree they are merely a proximate consequence of forced karst use (Pounds, 1991 as cited in McGraw, 1996). McGraw (1996) has shown that colobine species show consistent locomotor behavior across habitats with different structures. Unlike McGraw, however, I would not expect to find that Delacour's langurs express the same frequency of leaping and climbing in a non-karst habitat, for example, the forested valleys between some remaining karstic habitat. The reason for that prediction is obvious: a non-karstic habitat would not have as much exposed rock as VLNR does and therefore the differences in substrate availability would be too great (unlike in McGraw's study) to prevent change. Despite evolution for arboreal quadrupedalism and leaping, the flexibility and *totipotentiality* of colobine morphology permits locomotor *habit* adjustments in a mostly non-arboreal environment.

Locomotor behavior in primates might be highly conservative regardless of structural habitat differences (*Saguinus mystax*: Garber and Pruetz, 1995; *Colobus badius,* C. *polykomos, C. verus, Cercopithecus diana,* and *C. campbelli:* McGraw, 1996), except under circumstances of extreme habitat variability, such as limestone karst habitat. That Delacour's langurs do not leap at Van Long Nature Reserve is probably not a function of their body size but rather of their support type. Quantifying the structural habitat at Van Long will be essential to determine substrate preference. Ideally, future studies would examine the Delacour's langur in non-restricted karst habitat to determine and compare the frequency of leaping and climbing behaviors where rocky substrates are not as commonly available. It seems unlikely, however, that for the foreseeable future there will be a site other than Van Long Nature Reserve where the locomotion of this critically endangered colobine can be quantified.

8.5 Appendix

Table 35: Total locomotor and postural behaviors observed for Delacour's langurs at Van Long Nature Reserve from June 2007-July 2008

	Male	Female	Female with baby	Subadult
Locomotions				
Bound	X	X	X	X
Vertical climb	X	X	X	X
Quadrupedal walk	X	X	X	X
Headfirst descent	X	X	X	X
Bipedal hop	X	X	X	X
Orthograde move	X	X	X	X
Unimanual swing	X	X	X	X
Rumpfirst descent	X	X	X	X
Pronograde leap	X	X	X	X
Straddle wedge		X	X	
Bimanual drop	X	X	X	X
Gallop	X	X	X	X
Pronograde move	X	X	X	X
Quadrupedal drop	X	X		X
Poleslide		X		
Branch run	X	X	X	X
Bimanual swing		X		
Bimanual pullup		X		
Scramble		X		
Orthograde leap		X	X	
Bipedal walk		X	X	
Scoot		X		
Postures				
Sit in	X	X	X	X
Sit out	X	X	X	X
Quadrupedal stand	X	X	X	X
Leg hang	X	X		
Chair sit	X	X	X	X

Table 35, continued

Sit prop	X	X	X	X
Full crouch	X	X	X	X
Side lie	X	X	X	X
Bipedal stand	X	X		X
Belly lie	X	X	X	X
Vertical cling	X	X	X	X
Forelimb crouch	X	X	X	X
Hindlimb crouch	X	X	X	X
Squat		X		
Straddle	X	X	X	X
Quadrupedal suspend		X		X

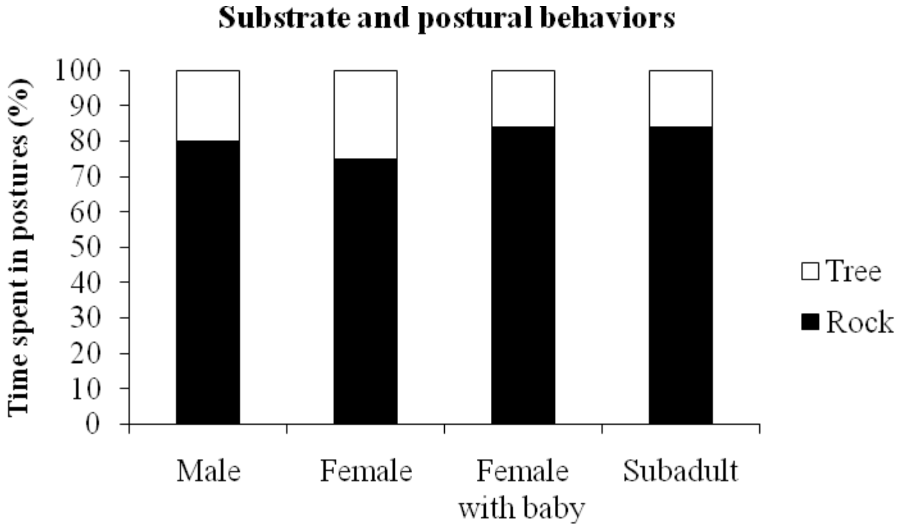

Figure 37: Time spent in postural behaviors on trees and rocks by age/sex class

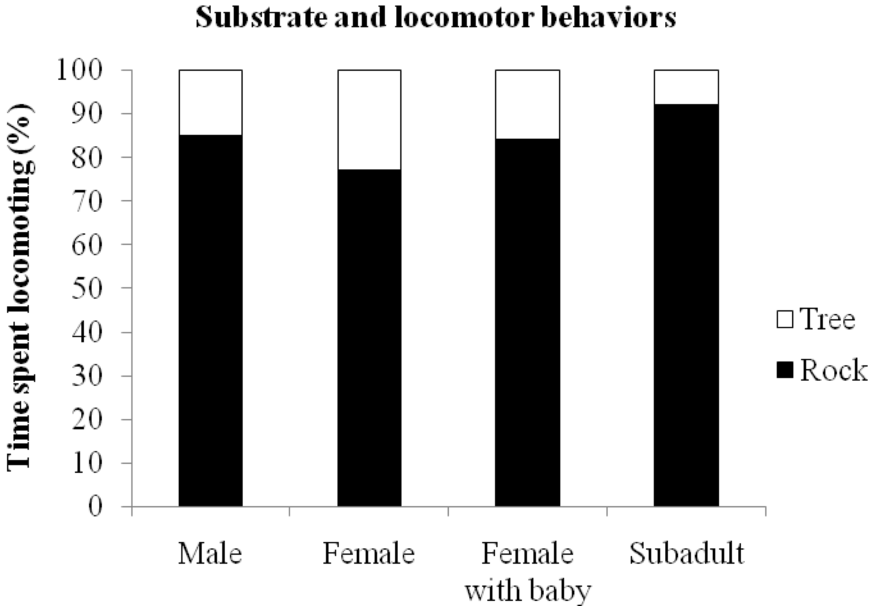

Figure 38: Time spent in locomotor behaviors on trees and rocks by age/sex class

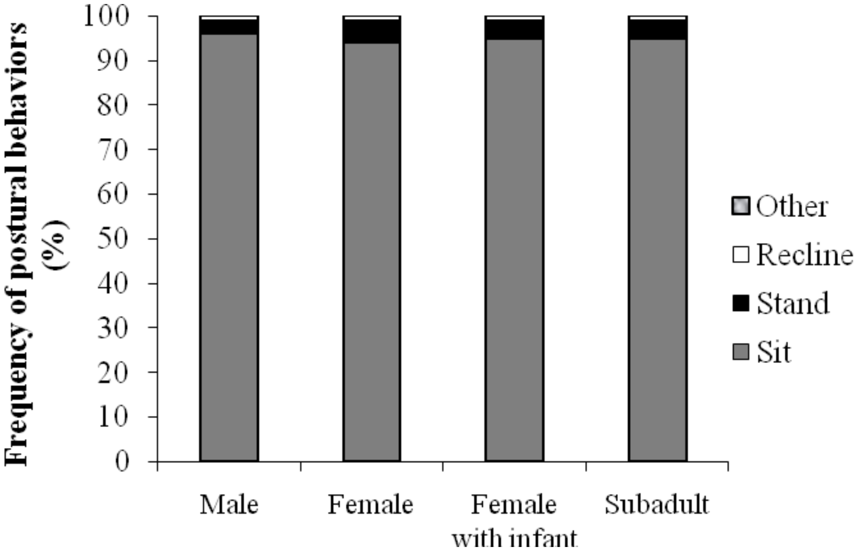

Figure 39: Postural frequencies by age/sex class

9. Conclusion

In this study, I quantified the foraging ecology of Delacour's langurs living on Dong Quyen Mountain in Van Long Nature Reserve, Vietnam to address if these langurs show special adaptations to limestone karst or if they are exploiting a refuge habitat into which they have been pushed. I quantified their foraging ecology by systematically investigating their diet and feeding ecology, the chemisty of their eaten leaves, and the locomotions and substrates they utilized. In this chapter, I summarize the results presented in Chapters 5 through 8 and discuss how they inform our understanding of the natual history and current distribution of limestone langurs. I also incorporate suggested future research directions. I conclude this dissertation with a discussion of how this study's results impact current conservation assessments and future conservation actions for the critically endangered Delacour's langur.

9.1 Summary of Results

9.1.1 Diet and Feeding Ecology

From August 2007 through July 2008, the diet of Delacour's langurs on Dong Quyen Mountain, Van Long Nature Reserve was dominated by young leaves monthly, seasonally, and annually. The annual diet consisted of nearly 79% foliage with almost 60% young leaves. Despite a distinct wet and dry season over the study period, seasonal variation in plant part consumption was slight. Fruit and seeds were a small contribution to the diet. Delacour's langurs ate 42 of 145 available species, and they concentrated on a subset of this number. Five plant species comprised more than 60% of the diet and 16 species comprised more than 93%. More than half of the diet came from climbers, and climbers were over-eaten based on their availability in the habitat.

Delacour's langurs are among the most highly folivorous of studied colobines, and- along with the closely related *T. leucocephalus* of southern China- the most folivorous of the Asian langurs. Whether high folivory is due to a lack of available fruits and seeds in limestone habitats is unknown. What is certain, however, is that the plant species most important in the Delacour's langurs' diet at VLNR throughout the study were not plants endemic to limestone. Thus, feeding dependence alone therefore cannot explain the current distribution of limestone langurs on karst habitat.

9.1.1.1 Future Research Directions

That Delacour's langurs do not rely on limestone endemics does not necessarily mean that they have been pushed recently into karst habitat as refuge. Data are needed to test the other hypotheses concerning limestone langur distribution: use of caves for protection from predators; use of caves for shelter against climatic conditions; and the presence of water. *Trachypithecus francoisi* seem to choose caves and ledges as sleeping sites based mainly on the proximity of the sleeping place to their feeding sites, and not for either resource defense or comfort; data were equivocal in supporting predator defense (Zhou et al., 2009b). Over the study period, Delacour's langurs slept high and low on Dong Quyen Mountain; they slept in caves and on exposed rock surfaces.

Anecdotally, it seemed that the langurs slept nearest to where they were feeding, rather than away from humans or protected from weather. Future studies should quantify this sleeping site behavior.

Now that the important foods in the Delacour's langur diet are known, these species and individual plants should be monitored to gain an understanding of availability and usage of food resources. Intensive monitoring of food availability and use will indicate food preference and selectivity (Marshall and Wrangham, 2007). Better data on food distribution, abundance, seasonality, availability should also be related with group size, day range length, intergroup interactions, competition, and reproduction to inform demographic and life history parameters. These data can also be used to address questions of whether within-group scramble competition and the ecological constraints model apply to this colobine in this habitat (Snaith and Chapman, 2007). More data on temporal changes in home range and day range –gained through innovative methodological approaches (Ren et al., 2008: *Rhinopithecus bieti*) - should also be related to food distribution and seasonality. When compared with activity budget data across years, on-going phenological and dietary monitoring should elucidate patterns between food availability, habitat use, and ranging patterns.

9.1.2 Chemistry of Plants and Soils

Overall, this study supports protein:fiber ratio as a good predictor of leaf choice for relatively small mammalian herbivores, including primates (Milton, 1979), and as a strong indicator of colobine leaf selection across the Paleotropics. Over the study period, Delacour's langurs ate leaves with high protein:fiber ratios, though neither protein nor fiber alone were different between eaten and uneaten leaf samples. Feeding samples from the most frequently consumed species in the diet contained lower amounts of condensed tannins and total phenolics than the less frequently consumed food species, suggesting defensive compounds negatively influence primate food choice.

Soils on the Dong Quyen Mountain of Van Long Nature Reserve were neutral (pH 7) with low sand content (15.7%) and high P, K, Mg, and Ca levels compared to other colobine sites. The percentage of carbon in the soils is ten times that of nitrogen, and yet young leaf availability never fell below 40% throughout the study period. Plants are clearly capable of producing new growth in this habitat. Van Long contains mostly secondary and regenerating growth. Coley (1983) found that pioneer species have faster growth rates (investment in growth over defense), less tough leaves, and lower concentrations of fiber, and higher protein:fiber ratios. Secondary and recovering forests – such as Van Long - may therefore have sufficient or even high food availability which correlates with colobine biomass (Wasserman and Chapman, 2003).

9.1.2.1 Future Research Directions: Ecological Determinants of Delacour's Langur Biomass and Density

Concluding that protein:fiber ratio is an important determinant of food choice in limestone habitats, I wanted to further apply my findings to ecological determinants of biomass. Mature leaf protein-to-fiber ratio has been shown to be a good indicator of colobine biomass in both Africa and Asia (Davies, 1984; Waterman et al., 1988; Chapman and Chapman, 2002; Chapman et al., 2002b), and as mature leaf quality improves, colobine biomass increases (Davies, 1994). Biomass might also be influenced by a species' ability to tolerate low quality foods during periods of resource scarcity (Chivers, 1974), indicating a species' behavioral flexibility.

Delacour's langur biomass is extremely low compared to other colobines, yet the population density at Van Long is within the range of other colobine sites. Colobine biomass at VLNR is 1.82 kg/ha, compared to 25 kg/ha at Polonnaruwa, Sri Lanka and 18.24 kg/ha at Kibale, Uganda. Delacour's langur population density at VLNR is 26.4 individuals/ km^2 compared with 15 individuals/km^2 for *Presbytis rubicunda* in northern Borneo and 315 for *Colobus guereza* in Bole, Ethiopia (Davies, 1994). Within Kibale, *Colobus guereza* averages 12 individuals/km^2 while *Procolobus badius* averages 300/km^2 (Struhsaker and Leland, 1987). In both Asia and Africa, as mature leaf quality improves, colobine biomass increases (Davies, 1994).

Unfortunately, without community-wide data on mature leaf protein:fiber composition, I am unable to discuss how leaf quality may contribute to low colobine biomass at Van Long. Further, a decimation of the population from hunting, as noted earlier, also precludes a purely ecological explanation of current density and biomass. Future studies could fill this important hole. Habitat-wide plant chemistry data are helpful in determining carrying capacity and therefore would be important to inform future translocation projects at Van Long (see below).

Future studies on limestone langurs' nutritional ecology would benefit from some methodological adjustments. First, the next study would do well to include a more comprehensive analysis of phytochemicals and nutrients (eg saponins, alkaloids, terpenes, glycosides, carbohydrates, flavonoids, lipids, vitamins, etc.) to gain a more complete picture of chemicals influencing food selection. Second, a future study on the chemistry of Delacour's langur foods should also include acid detergent fiber (ADF) in addition to NDF to facilitate comparisons across studies. Third, future studies should consider the use of near-infrared reflectance spectroscopy (NIRS) as a quick and inexpensive way to assess nutritional chemistry and allow intraspecific comparisons of vegetation samples (Rothman et al., 2009). Finally, Delacour's langurs drank water more frequently in the morning than the afternoon. Animals drink water to help flush out plant toxins and detoxify high levels of secondary compounds (Mattson, 1980; Coley, 1983), and so it would be interesting in the future to analyze phytochemical differences between foods eaten in the morning and afternoon.

Future studies should also incorporate tests of the mechanical properties of Delacour's langur foods, as has been done for this species in captivity at the Endagered Primate Rescue Center (Wright et al., 2008b). Plant toughness is frequently used as a proxy for fiber content (Coley and Barone, 1996). Since Delacour's langurs are eating leaves with lower fiber levels compared to other colobines (Chapter 6), they may also be eaten items that are less tough than non-eaten items. Future studies should include mechanical properties as well as additional chemical constituents to gain a fuller picture of factors influencing langur food choice in a limestone karst habitat.

9.1.3 Activity Budget and Positional Behavior

9.1.3.1 Activity Budget, Locomotion, and Economy of Energy

From June 2007-July 2008, Delacour's langurs were predominantly quadrupedal. While they were highly 'terrestrial' in their use of rocks and in leaping less than other African and Asian colobines, their morphology (intermembral index) does not suggest terrestrialism. Further, terrestrialism does not adequately describe the locomotion of these langurs. These are cliff-climbing langurs, moving on a dangerous substrate that offers distinctly different pressures from those of a typical terrestrial substrate. These data do not support an evolutionary adaptation for limestone karst.

Throughout the study period, resting accounted for 61.3% of the Delacour's langur activity budget, with the rest of daytime hours divided between feeding (28.2%), socializing (6.3%), and traveling (4.2%). Though it was the smallest contribution to the activity budget from June 2007-July 2008, locomotion in the limestone habitat requires caution and deliberation and is likely energetically costly. Delacour's langurs are among the least active colobines for which there are data, a result which may be due, in part, to this highly folivorous taxon conserving energy in an energetically-demanding habitat.

Economy of energy is found in many species that eat a high-foliage diet (*Colobus guereza*: Oates, 1977; *Colobus polykomos*: Hladik, 1977; *Trachypithecus vetulus*: Stanford, 1991; *Trachypithecus pileatus*: Dasilva, 1992; *Trachypithecus leucocephalus*: Huang et al., 2003; *Rhinopithecus bieti*: Ding and Zhao, 2004). Going up and down steep terrain is energetically more expensive than traversing gentle slopes or flat ground, and animals show increased costs when moving vertically versus horizontally (Hanna, 2006).

Investigations on the energetic costs of another mountain-dwelling mammal, free-ranging goats (*Capra hircus*) living in the Filabres Mountains of Spain (Lachica et al., 1997) have found that the energetic cost of locomotion (distance traveled, vertical ascent and descent) contributes a substantial amount to total energy expenditure (Lachica et al., 1997). Captive studies of goats have corroborated these field observations. Goats trained to run on a treadmill used more than twice the amount of energy (from 1.91 to 6.44 J kg−1 BWm−1) when the slope of the treadmill was increased from -10 to +10 (Lachica and Aguilera, 2003). Even a small gradient increase raised energy costs. Energy costs of walking by goats were estimated to be lowest for descending locomotion; as the gradient increased the efficiency of goat locomotion decreased (Lachica and Aguilera, 2003).

While locomotion is a small component of the Delacour's langur activity budget at Van Long, langurs travel quadrupedally up and down the sides of mountains on a daily basis, employing tremendous leaps and bounds across rock surfaces as well as rock-climbing sheer vertical faces. These substrates do not offer the flexibility and ability for energy capture of arboreal substrates. Dong Quyen Mountain peaks at 428 meters. On several observation days, focal groups were recorded traveling from the top of the mountain down to <20 meters of the mountain's base and then ascending the mountain at the day's end. In addition, two known sleeping sites of one focal group were located along the base of the mountain. The group would sleep next to the wetland and then ascend to be out of view over the top of the mountain before nightfall. Due to the stunted nature of plants, most of the vertical ascent occurs on exposed rock and climbers growing over rock.

During the study period, the average day path length of Delacour's langurs was 476 meters (range: 230-978 meters; N=16 days). Though number of sample days is small, day length seemed to increase in the winter months when young leaves were least available, perhaps suggesting that langurs increased travel during times of scarcity, expending more energy in search of available food. This study is incapable, however, of making such an assessment, because I only used days when the langurs were fully visible from dawn to dusk (N=16 days). I had to use Global Positioning System approximations since I was unable to access everywhere that the langurs traveled.

9.1.3.2 Future Research Directions: Travel Lengths and the Energetic Costs of Locomotion

An exciting future area of research for the limestone langurs is energy expenditure: how do a highly folivorous diet, the energetic costs of locomotion, and the distribution of resources relate in this environment? Now that we have a baseline as to what plant species are important in the langurs' diet, future studies should quantify the seasonal availability and distribution of these food resources across the landscape (through additional transects and the addition of box plots (Ganzhorn, 2003) and their relationship with seasonal ranging and habitat use, especially the verticality of travel. Primatologists have likely been underestimating the costs of a vertical and three-dimensional environment in ranging analyses (Digby, 2008; Glander, personal communication).

Future studies would also benefit from methodological adjustments. I collected locomotor bout data without distance, yet including distance with locomotor bout data is most accurate (Fleagle, 1976; Doran, 1992, 1993a) and is the best method to determine energy expenditure during locomotion (Fleagle, 1978). In addition to distance, a more detailed analysis of positional behavior would include angle, size, and height of substrate. In addition to the bout method, data should be collected using instantaneous time sampling (Garber, 1984; Cant, 1986; Boinski, 1989; Hunt, 1992) at 3 minute intervals to protect against data dependency (Dagosto, 1994; McGraw, 1998b) to compensate for the deficiencies of both methods (Doran, 1992). Finally, future studies should quantify the amount of rock versus vegetation cover in the habitat to determine selectivity of support type.

9.2 Conservation of Delacour's Langurs

The results from this study do not support the Delacour's langurs as being evolutionarily adapted for limestone karst. Rather, the feeding and locomotor data suggest that this is a flexible taxon capable of successfully reproducing within a fragmented island habitat into which it has been pushed.

Protected from hunting, the Dong Quyen Mountain subpopulation has rebounded from 35-40 langurs in 2000 to about 70 langurs in 2008. Over the course of the study period, 15 infants were born on Dong Quyen (and 14 survived). In August 2008, the total population of Van Long Nature Reserve was about 90 individuals.

The results of this study force us to question the so-called 'quality' of karst habitat. For folivores, this habitat may be more productive – and therefore better quality- than has been assumed. Despite the stunted vegetation and dangerously sharp limestone, an asynchronous flushing produces year-round availability of young leaves. Ripley (1979) has suggested that consistent edible foliage, from young leaf flushing, might contribute to high primate folivore biomass. This young leaf availability on Dong Quyen- along with a lack of hunting within the reserve- may provide the potential for a high colobine biomass. The number of babies (14) that were born on Dong Quyen Mountain during the study period supports this suggestion.

9.2.1 Threats to Remaining Delacour's Langurs

In recent years, illegal hunting for China and Southeast Asia's thriving bushmeat industry has been the largest threat to this species, and to most wildlife in the region. Langurs are hunted for the use of their bones, organs, and tissue in traditional medicine. Over ten years of surveys and monitoring by the Frankfurt Zoological Society, a minimum of 30 Delacour's langurs were hunted per year for a total of 320 killed animals (Tilo Nadler, personal communication). The poaching situation has been even worse for the Cat Ba langur (*Trachypithecus poliocephalus)*, whose population of 2,000-2,500 in the 1960s declined 98% to only 53 animals by 2000; today, just 10 Y-chromosomes exist for this species (Tilo Nadler, personal communication). For isolated unimale social groups, the loss of the adult breeding male would have a devastating impact that on the group.

The likely final extirpation of *Hylobates lar* from China is due to uncontrolled hunting, even within nature reserves (Grueter et al., 2009b). Indeed, despite a protected langur population at Van Long, indiscriminate snare hunting persists in the more distant and less patrolled regions of the reserve. In May 2008, Le Van Dung recovered five snare traps while conducting survey work in Van Long's northwest region (Figure 40). While these snares were likely not intended for nor would have caught langurs (they were found on footpaths in the valleys between karsts), the recovery of them is a reminder that populations are surrounded by intense human pressure.

Figure 40: Five metal snare traps were recovered from the northwest region of Van Long Nature Reserve in May, 2008.

Despite a cessation in hunting at Van Long, the composition of these groups might be shifting for some years, and therefore what I observed during the study period may or not be the natural social organization of this species. I observed unimale and multimale langur groups at Van Long, as well as one bachelor group and at least one solitary migrating male. Territories were overlapping, but boundaries were defended by males, who often chased neighboring males in border areas. Colobines are generally characterized by having overlapped ranges and matrilineal groups with one resident male (Newton and Dunbar, 1994). Most colobines form matrilineal groups of 7-20 animals with one resident male and other males leaving before adulthood. However, colobines also form unimale-multifemale and multimale-multifemale social units, as well as all-male bachelor groups which periodically raid social groups for mating opportunities (though see Korstjens et al., 2005). The 'typical' organization and dispersal system of this species should be interpreted with caution. Interesting questions about the sociality of this species remain to be studied.

Despite the persistent threat of hunting, Southeast Asia's limestone langurs now face a larger threat: the decimation of their economically valuable refuge habitat. Limestone karsts serve as biodiversity reservoirs or "arks" with high levels of endemism. While Southeast Asia has the highest rate of natural habitat loss among the tropics (Sodhi and Brook, 2006), karsts have historically been protected because they are not amenable to agricultural development (Clements et al., 2006). That the valleys between karsts have been converted to rice agriculture while the rocky outcrops have persisted is the major reason that karst is considered refugia. The status of karst as refuge is rapidly changing, however.

The quarrying of limestone for cement now represents the largest threat to limestone species (Sodhi and Brook, 2006). Many of Southeast Asia's karsts are located within biodiversity hotspots (Myers et al., 2000) but weak legislation, commercial and economic interests, and a lack of scientific data have left these fragile habitats vulnerable (Clements et al., 2006). VLNR is experiencing limestone quarrying all around its borders

(Figure 41). The blasting has affected ranging patterns, with groups spending less time on the northeast side of Dong Quyen, pushing groups into closer contact with one another (personal observation). An important area of conservation management research will be monitoring the relationship of quarrying along Van Long's borders with the ranging of groups within the reserve.

Figure 41: Blasting of limestone mountains (for cement) now poses the greatest risk to remaining limestone langur habitat and its inhabitants

9.2.2 Conservation Going Forward: Reintroduction and Research

9.2.2.1 Reintroduction at Van Long Nature Reserve

Captive breeding and reintroduction have brought species back from the brink of extinction. Several examples exist of animals rebounding from extremely low numbers, and there are examples of founder populations which gave rise to large mammal populations (Benirschke and Kumamoto, 1991). Strict protection in a reserve and translocation brought back the white rhino (*Ceratotherium simum*) from only ten individuals at the turn of the 20th century to more than 120 by 1930 (Caughley, 1994). The Arabian oryx (*Oryx leucoryx*) was extinct in the wild in 1972, but captive breeding of nine founder individuals brought the population back to 105 in only four years (Ostrowski et al., 1998). The cheetah (*Acinonyx jubatus*) suffered from inbreeding depression and at least one genetic bottleneck leading to low heterozygosity and concerns for population viability (O'Brien et al., 1985). Despite ongoing threats from human conflicts and the lack of self-sustaining captive breeding programs, there are estimated 10,000 cheetahs in the wild today (although exact numbers are unknown). Finally, only a few dozen Mongolian wild horses (*Equus ferus przewalkskii*) existed in the 1940s, yet by the 1980s captive breeding programs brought their numbers up to 1,500, several hundred of which have been released back into Mongolia (Klesius, 2006). For protected Delacour's langurs, a sex ratio skewed towards females should permit a faster population rebound (Caughley, 1994).

The Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam is the only captive facility in the world that breeds Delacour's langurs. There are now 17 individuals at the EPRC. For several years, the EPRC has been interested in and working with the Vietnamese government to reintroduce a Delacour's langur group to a safe place in the wild. Van Long is the natural place for reintroduction, as langurs can be monitored from boats and the area is relatively easy to patrol since it is circumscribed by water. The EPRC has considered releasing the designated group to Dong Quyen Mountain. However, the results of this study show that the langurs on Dong Quyen are reproducing nicely in the absence of human interference. The population on Dong Quyen has nearly doubled in eight years. I have suggested that the langurs here be left alone to continue their rebound. Delacour's langurs from the EPRC will therefore be released to the northwest region of Van Long, a more forested, yet less protected, part of Van Long.

9.2.2.2 Field Research on Rare Langurs Is Needed Now More Than Ever

Despite diminishing funding for basic research, we urgently need population surveys and natural history data to inform conservation management (Fashing, 2007). Fashing (2007) further notes that many of the world's endangered colobines have yet to be the focus of one basic ecological study (Fashing, 2007). Delacour's langurs currently exist in small and isolated subpopulations. Modeling suggests and data show that rare species are the most extinction-prone (Terborgh and Winter, 1980), small population best predicts extinctions (Diamond, 1984) and extinction risk increases with decreased island area (MacArthur and Wilson, 1967; Hope, 1973; Nitecki, 1984; Lovejoy et al., 1984).

Conservation biologists want to know about the process of decline for both the range and numbers of a species as well as how to prevent further losses (Soule, 1983). A key issue in primate conservation is determining primate communities and their use of resources, to then use in management and policy-making (Gupta and Chivers, 1999). Further study is needed on the habitat requirements, the range of habitat quality and size, and the amount of anthropogenic perturbation that *Trachypithecus delacouri* will endure. Despite a population increase at Van Long, the future of the Delacour's langur remains grim. It is important to collect and document data on their natural behaviour and ecology in the wild, so that if and when we lose this species, we know what we have lost. The purview of conservation biology calls us to continue this research.

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Biography

Catherine Workman was born on February 17, 1979 in Anderson, Indiana. From 1997-2001, she attended the University of Colorado, Boulder and graduated summa cum laude with a double degree in anthropology and English literature. She obtained a Master's of Arts in anthropology from the University of Colorado, Boulder (2002-2004). Catherine earned a PhD in the Department of Evolutionary Anthropology from Duke University in 2010.

Since obtaining her bachelor's degree, Catherine has received a number of honors. Her teaching evaluations were among the top 5% of all undergraduate instructors at Duke University in Fall, 2009. She gave the commencement address at The Harpeth Hall School in Nashville, TN in May, 2009. Catherine was awarded 4th place (out of 151) for oral presentation in the International Primatological Society Student Competition in Edinburgh, Scotland in 2008. She received the National Science Foundation Graduate Research Fellowship Honorable Mention in 2005. She is a member of the Sigma Xi Scientific Research Society.

Published articles and book chapters:

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