The Conservative Nature of Primate Positional Behavior: Testing for Locomotor and Postural Variation in *Colobus vellerosus* and *Cercopithecus campbelli lowei* at Boabeng-Fiema Monkey Sanctuary, Ghana

Dissertation

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

Robert Luken Schubert, M.A.
Graduate Program in Anthropology

The Ohio State University
2011

Dissertation Committee
W. Scott McGraw, Advisor
Debbie Guatelli-Steinberg
Dawn Kitchen
Jeffrey McKee
Abstract

Several recent field studies have shown that primate posture and locomotion exhibit minimal intraspecific variation. Between January and November 2009, I collected data on positional behavior and habitat use via three-minute instantaneous focal observation of the ursine colobus (*Colobus vellerosus*) and Lowe's monkey (*Cercopithecus campbelli lowei*) at the Boabeng-Fiema Monkey Sanctuary (BFMS), Ghana. I sampled quantitative ecological data on canopy density, understory density, tree size and average number of large trees in two areas of forest characterized by differing degrees of anthropogenic disturbance. Using Row x Column statistical comparisons (G-tests, Fisher Exact Tests), I tested for significant intraspecific variation in postural and locomotor profiles for females of each species living in these forest areas. For both species, forest strata, support size, support orientation and postural profiles differed significantly between these forests. Locomotor profiles differed significantly between forests only for guenons. I argue that the mosaic nature of more disturbed forest at BFMS reduced the number of direct, upper canopy arboreal pathways and resulted in more frequent use of lower and thinner supports for both species. Intraspecific postural and locomotor contrasts between habitats are considered in the context of body mass support, balance, and diet. *Colobus* locomotor consistency may be a product of both their
larger body size and leaping specializations of their postcrania. I also tested for significant sex-based differences in positional behavior for both species. While my male dataset was limited, significant differences in overall postural and locomotor profiles were evident. I argue that contrasting nutritional requirements, social roles, and body sizes between the sexes for both species underlie these contrasting positional behavior profiles. While statistical differences in postural (both guenons and colobus) and locomotor profiles (guenons) may be ecologically significant, the differences identified in this study pose little threat to established form-function associations in primates and support the notion that primate positional behavior is largely conserved across sexes and habitats.
Dedication

Dedicated to my wife, Valerie. Thanks for your love and encouragement. And to Huck, that we can explore the forests of the world together one day.
Acknowledgements

I would like to thank my advisor, Dr. Scott McGraw, and the rest of my dissertation committee for their feedback and encouragement both in this project and throughout my graduate career. I also thank Dr. Pascale Sicotte, her students, and Erik Lindquist for helping to facilitate this project and familiarizing me with the site and surrounding communities. I especially thank all the individuals in the communities of Boabeng and Fiema, particularly the fetish-priests and chiefs of the two communities, for welcoming me to their homes, allowing me access to their forests, and assisting me in my research. I thank Valerie Moring Schubert for helping to produce this document, for assisting in fieldwork, and for her photographic contributions. I would also like to thank The Ohio State University Graduate School for partially funding this project through the Alumni Grants for Graduate Research and Scholarship. Finally, I would like to thank my family, particularly my mother, Barbara Hinson, and uncle, Robert Luken for helping to support this project and inspiring me to follow my dreams no matter where they might take me.
Vita

2001.............................................................. B.A. Anthropology, University of Illinois

2004.............................................................. M.A. Anthropology, The Ohio State University

2003–Present ............................................ Graduate Teaching Associate, Department of

Anthropology, The Ohio State University

Fields of Study

Major Field: Anthropology
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The Conservative Nature of Positional Behavior</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Boabeng-Fiema Monkey Sanctuary</td>
<td>21</td>
</tr>
<tr>
<td>3</td>
<td>Forest Differences and Study Groups</td>
<td>50</td>
</tr>
<tr>
<td>4</td>
<td>Methods of Sampling and Analysis</td>
<td>76</td>
</tr>
<tr>
<td>5</td>
<td>Forest Strata and Support Usage</td>
<td>98</td>
</tr>
<tr>
<td>6</td>
<td>Intraspecific Differences in Posture</td>
<td>127</td>
</tr>
<tr>
<td>7</td>
<td>Intraspecific Differences in Locomotion</td>
<td>161</td>
</tr>
<tr>
<td>8</td>
<td>Intraspecific Sex Differences</td>
<td>202</td>
</tr>
<tr>
<td>9</td>
<td>Project Summary and Significance</td>
<td>257</td>
</tr>
<tr>
<td></td>
<td>References</td>
<td>278</td>
</tr>
<tr>
<td></td>
<td>Appendix A: Postural and Locomotor Behaviors Illustrated</td>
<td>289</td>
</tr>
</tbody>
</table>
List of Tables

Table 1.1: Results of Intraspecific Studies of Positional Behavior.............................................19
Table 3.1: Forest Plots in Colobus Home Ranges....................................................................65
Table 3.2: Small Tree Stand Density in Colobus Home Ranges..................................................67
Table 3.3: Forest Plots in Guenon Home Ranges.......................................................................69
Table 3.4: Small Tree Stand Density in Guenon Home Ranges.....................................................71
Table 4.1: Locomotor and Postural Behaviors Defined.............................................................86
Table 4.2: Illustration of R x C Statistical Tests.........................................................................95
Table 5.1: Predictions for Intraspecific Differences in Habitat Usage.................................100
Table 5.2: Body Mass for Female C. campbelli lowei and C. vellerosus.................................102
Table 5.3: Support Type Categories.........................................................................................109
Table 5.4: Support Orientation Categories..............................................................................111
Table 5.5: Statistical Comparisons of Habitat Usage Profiles..............................................112
Table 5.6: Female Colobus and Guenon Forest Strata Profiles.............................................113
Table 5.7: Female Colobus and Guenon Support Type Profiles............................................115
Table 5.8: Female Colobus and Guenon Support Orientation Profiles...............................117
Table 6.1: Predictions for Intraspecific Variation in Postural Profiles..................................129
Table 6.2: Diet and Body Mass of C. vellerosus and C. campelli lowei..................................132
Table 6.3: Posture-Associated Maintenance Activities............................................................135
Table 6.4: Recorded Postural Categories ................................................................. 136
Table 6.5: Lumped Postural Categories ................................................................. 137
Table 6.6: Overall Postural Profiles for Female Colobus ....................................... 139
Table 6.7: Overall Postural Profiles for Female Guenons ..................................... 140
Table 6.8: Results of Female Postural Profile Comparisons .................................. 141
Table 6.9: Postural Profiles of Female Colobus during Rest .................................. 142
Table 6.10: Postural Profiles of Female Guenons during Rest ............................... 143
Table 6.11: Forest Strata Profiles of Common Postures for C. vellerosus ............. 144
Table 6.12: Forest Strata Profiles of Several Postures for C. campbelli lowei ....... 149
Table 6.13: Postures Ranked by Overall Frequency ............................................ 158
Table 7.1: Predictions for Intraspecific Locomotor Differences ........................... 166
Table 7.2: Locomotion-Associated Maintenance Activities ................................. 171
Table 7.3: Recorded Locomotor Categories ......................................................... 172
Table 7.4: Pooled Locomotor Categories .............................................................. 174
Table 7.5: Overall Locomotor Profiles for C. vellerosus ........................................ 175
Table 7.6: Overall Locomotor Profiles for C. campbelli lowei ............................... 176
Table 7.7: Locomotor Profiles for C. campbelli lowei during Non-Social Locomotion ............................................................................................................. 178
Table 7.8: Forest Strata Profiles of Locomotor Behaviors during Non-Social Locomotion for C. campbelli lowei ................................................................. 180
Table 7.9: Forest Strata Profiles for C. vellerosus during Non-Social Locomotion .... 188
Table 7.10: Ranked Preference of Locomotor Behaviors for C. campbelli lowei ...... 199
Table 8.1: Predictions for Sex-based Differences in Wawa Colobus Positional Behavior
........................................................................................................................................................................... 208
Table 8.2: Predictions for Sex-based Differences in Guenon Positional Behavior...
........................................................................................................................................................................... 208
Table 8.3: Male and Female Body Mass for *C. vellerosus* and *C. campbelli lowei*...... 210
Table 8.4: Results of Sex-based Intraspecific Comparisons of Postural and Locomotor Profiles for Guenons and Colobus in Unlogged Western Forest .......... 218
Table 8.5: Overall Postural Profiles for Male and Female Wawa Colobus.............. 219
Table 8.6: Overall Locomotor Profiles for Male and Female Wawa Colobus......... 220
Table 8.7: Positional Behavior of Male and Female Wawa Colobus During Seven Maintenance Activities .......................................................................................................................... 221
Table 8.8: Overall Postural Profiles for Male and Female Central Guenons ............ 224
Table 8.9: Overall Locomotor Profiles for Male and Female Central Guenons ....... 225
Table 8.10: Positional Behavior of Male and Female Central Guenons During Seven Maintenance Activities .......................................................................................................................... 226
Table 8.11: Forest Strata Profiles for Male and Female Wawa Colobus During Active Feed........................................................................................................................................................................... 234
Table: 8.12: Male and Female Wawa Colobus Support Size Profiles...................... 236
Table 8.13: Forest Strata Profiles for Male and Female Wawa Colobus .................. 244
Table 8.14: Forest Strata Profiles for Male and Female Central Guenons .............. 247
Table 8.15: Ranked Male and Female Postures and Locomotor Behaviors ............. 253
Table 9.1: *C. vellerosus* Habitat Usage and Positional Behavior........................... 259
Table 9.2: *C. campbelli lowei* Habitat Usage and Positional Behavior............... 259

x
Table 9.3: Summary of *C. vellerosus* and *C. campbelli lowei* Habitat Use, Postural and Locomotor Comparisons ................................................................. 264

Table 9.4: Sex-Based Postural and Locomotor Differences for Colobus and Guenon ........................................................................................................... 268

Table 9.5: Vertical Distribution of Wawa Colobus Locomotor Behaviors .......... 275
List of Figures

Figure 1.1: Influences on Positional Behavior.................................................................5
Figure 1.2: Primate Positional Behavior Variation Across Habitats..............................14
Figure 2.1: Map of Ghana and BFMS...........................................................................22
Figure 2.2: Species Portraits.......................................................................................26
Figure 2.3: Guenon Scanning Surrounding Supports and Foliage in Dense
Understory................................................................................................................31
Figure 2.4: Domesticated Animals at BFMS.................................................................33
Figure 2.5: Monkey Cemetery ....................................................................................36
Figure 2.6: Ecotourism Attractions.............................................................................38
Figure 2.7: Village Raiding.........................................................................................42
Figure 3.1: Unlogged Western Forest...........................................................................51
Figure 3.2: Regenerating Farmland.............................................................................53
Figure 3.3: Wawa and Redtail Colobus Home Ranges................................................55
Figure 3.4: Central and Periphery Guenon Home Ranges.........................................57
Figure 3.5: Alternating Forest Plots Along Existing Trails.........................................59
Figure 3.6: Plot Sampling in Regenerating Farmland.................................................60
Figure 3.7: Canopy Density Estimates in Colobus Home Ranges..............................65
Figure 3.8: Vine Coverage in Colobus Home Ranges................................................66
Figure 3.9: Canopy Density Estimates in Guenon Home Ranges ........................................ 69
Figure 3.10: Vine Coverage in Guenon Home Ranges ............................................................. 70
Figure 3.11: Comparison of Western and Southern Forest Understories ................................. 72
Figure 5.1: *C. vellerosus* using Multiple Supports ................................................................. 105
Figure 5.2: Four Distinct Forest Strata at BFMS ................................................................ 107
Figure 5.3: Boughs, Branches, and Twigs Illustrated ............................................................... 109
Figure 5.4: Comparison of Female Colobus Forest Strata Use .................................................. 113
Figure 5.5: Comparison of Female Guenon Forest Strata Use .................................................... 114
Figure 5.6: Comparison of Female Colobus Support Type Profiles .......................................... 115
Figure 5.7: Comparison of Female Guenon Support Type Profiles .......................................... 116
Figure 5.8: Comparison of Female Colobus Support Orientation Profiles ............................... 117
Figure 5.9: Comparison of Female Guenon Support Orientation Profiles ............................... 118
Figure 6.1: Comparison of Overall Female Colobus Postural Profiles ...................................... 139
Figure 6.2: Comparison of Overall Female Guenon Postural Profiles ...................................... 140
Figure 6.3: Comparisons of Rest Postural Profiles for Female Colobus ................................. 142
Figure 6.4: Comparisons of Rest Postural Profiles for Female Guenons ................................. 143
Figure 6.5: Vertical Distribution of Common Postures for *C. vellerosus* ............................... 145
Figure 6.6: Twig-Associated *Sit* Postures for *C. vellerosus* .................................................. 148
Figure 6.7: Vertical Distribution of Several Postures for *C. campbelli lowei* ......................... 150
Figure 6.8: *Stand* Postures in Forest Understory ................................................................. 152
Figure 6.9: Guenon Foraging Postures ................................................................. 154
Figure 7.1: Comparison of Overall Locomotor Profiles for C. vellerosus ............ 175
Figure 7.2: Comparison of Overall Locomotor Profiles for C. campbelli lowei ....... 176
Figure 7.3: Comparison of Locomotor Profiles for C. campbelli lowei during Non-Social Locomotion ................................................................. 178
Figure 7.4: Regularly Traversed Canopy Gap by Southern Forest Guenons ............ 180
Figure 7.5: Comparison of the Vertical Distribution of Locomotor Behaviors during Non-Social Locomotion for C. campbelli lowei ........................................ 181
Figure 7.6: Southern Forest Understory .................................................................. 182
Figure 7.7: Guenon Climbing in Densely Interwoven Vine Tangles .................... 184
Figure 7.8: Undulating Southern Forest Understory ............................................. 186
Figure 7.9: Comparison of the Vertical Distribution of Locomotor Behaviors during Non-Social Locomotion for C. vellerosus ...................................................... 189
Figure 7.10: Colobus Bounding .............................................................................. 196
Figure 8.1: Visual Differences between Male and Female Guenons ..................... 215
Figure 8.2: Visual Differences between Male and Female Colobus ....................... 216
Figure 8.3: Comparison of All Postural Behaviors for Male and Female Wawa Colobus .............................................................................................................. 219
Figure 8.4: Comparison of All Male and Female Locomotor Behaviors for Wawa Colobus .............................................................................................................. 220
Figure 8.5: Comparison of All Postures for Male and Female Central Guenons ...... 224
Figure 8.6: Comparison of All Male and Female Locomotor Behaviors for Central Guenons .............................................................................................................. 225
Figure 8.7: Female *C. vellerosus* and Infant................................................................. 229

Figure 8.8: Comparison of the Vertical Distribution of Active Feed Observations for Male and Female Wawa Colobus ................................................................................................................................. 234

Figure 8.9: Comparison of Support Size Profiles for Male and Female Wawa Colobus Observations .................................................................................................................................................. 236

Figure 8.10: Female *C. campbelli lowei* and offspring .................................................. 237

Figure 8.11: Comparison of the Vertical Distribution of Male/Female Wawa Colobus Observations .................................................................................................................................................. 245

Figure 8.12: Comparison of the Vertical Distribution of Male/Female Central Guenon Observations .................................................................................................................................................. 247

Figure 8.13: Trail Use by Male *C. campbelli lowei* ......................................................... 251

Figure 9.1: Understory Feeding in *C. campbelli lowei* .................................................... 262

Figure 9.2: The Affects of Anthropogenic Disturbance on *C. vellerosus* and *C. campbelli lowei* Positional Behavior ................................................................. 266

Figure 9.3: Comparison of *C. campbelli campbelli* and *C. campbelli lowei* Postural Behaviors .................................................................................................................................................. 272

Figure 9.4: Comparison of *C. polykomos* and *C. vellerosus* Postural Behaviors ....... 272

Figure 9.5: Comparison of *C. campbelli campbelli* and *C. campbelli lowei* Locomotor Behaviors .................................................................................................................................................. 273

Figure 9.6: Comparison of *C. polykomos* and *C. vellerosus* Locomotor Profiles ....... 274

Figure A.1: *Cling* Postures .................................................................................................................. 290

Figure A.2: *Recline* Postures .................................................................................................................. 290

Figure A.3: *Sit* Postures .................................................................................................................. 291
Figure A.4: Stand Postures

Figure A.5: Horizontal Climbs

Figure A.6: Leaps

Figure A.7: Vertical Climbs

Figure A.8: Quadrupedalism
Chapter 1: The Conservative Nature of Positional Behavior

Although almost all nonhuman primates are able to perform, to a degree, those non-quadrupedal activities that, in the extreme, characterize a few highly specialized species (e.g., almost all primates are able to move bipedally on occasion, and can swing by their arms), nevertheless these chiefly arboreal animals are primarily quadrupedal in locomotor habit and have in general retained an anatomical format that is correspondingly adapted. (Oxnard, 1975, p. 21)

Non-human primates must negotiate a complex array of environmental, physiological and social challenges. These challenges involve acquiring desired food items, avoiding predators, finding mates, protecting offspring, and negotiating the complex social hierarchies of their species, among many others. To meet these challenges, primates are forced to make decisions every day stemming from how to best deal with the structural realities of their ecosystems (e.g., dealing with climatic changes, negotiating variable habitat structures, minimizing predation risks, competing with conspecifics over food and mates, accessing foods of differing properties and distributions) within the context of their own physiology (e.g., health, metabolic requirements, muscle fatigue) (Cant and Temerin, 1984).

As Oxnard’s (1975) quote introducing this chapter suggests, primates meet these daily challenges by displaying substantial behavioral flexibility; however, this flexibility is constrained by a bauplan, that save for significant ontogenetic alterations, derives from each species’ evolutionary history. Behavioral flexibility,
then, offers short-term solutions to everyday challenges posed by the environment but morphology constrains the likelihood that a given behavior is displayed. No matter how efficient leaping or brachiation might be, animals not morphologically equipped to efficiently use such locomotor strategies are unlikely to display them.

This study examines the intersection of morphology and environment and tests the degree to which the latter influences the postural, locomotor and habitat usage profiles for two cercopithecoid species: the ursine colobus (*Colobus vellerosus*) and Lowe's monkey (*Cercopithecus campbelli lowei*). I proceed by comparing behavioral data collected on groups of each of these species found in architecturally distinct forest habitats. I then compare the same profiles for males and females within each species to test for sex-specific positional behavior profiles. Below, I define positional behavior and describe several factors claimed to influence it.

**What is Positional Behavior?**

Prost (1965) established the classic dichotomy between locomotion and posture and collectively referred to these behavioral classes as a primate’s positional behavior. He distinguished these behavioral states by their differing degrees of body mass displacement. Hence, locomotion was defined as body mass displaced past a certain theoretical threshold while posture was defined as body mass displacement below that threshold. Therefore, posture is not necessarily defined as inactivity but could include muscle contractions with potentially
significant anatomical associations (e.g., standing, suspending from the forelimb or sitting all may involve significant muscle activity) (Rose, 1974). As a result, the line between where postural movements end and locomotor movements begin is not finely drawn. In practice, researchers of primate positional behavior typically associate locomotion with travel between physical locations while complete lack of motion, weight shifts, and slight limb movements without locality changes are collectively grouped into posture (e.g., Hunt et al., 1996).

**What Influences a Primate’s Positional Behavior?**

A primate’s positional behavior is tied to both its evolutionary history and its habitat in a relationship referred to as the Form-Function Complex (Bock and von Wahlert, 1965). Napier (1967) recognized the complexity of primate positional behavior and characterized it as a “T-shaped” phenomenon with a vertical axis representing the influence of phylogenetic history (i.e., inherited morphology) and a horizontal axis representing the influence of ontogeny (i.e., experience, habits, etc.). Habitat provides context vital for understanding the potential evolutionary advantages driving the selection of particular morphologies because morphological traits most often represent a compromise between the various activities with which they are associated (Bock and von Wahlert, 1965). For example, the morphology of the shoulder is associated with locomotion, manipulation, maintaining balance and many other daily activities with which a primate must contend and primates that perform those activities differently (e.g., leaping vs. climbing) all make use of the
same general anatomical structures. Many researchers have associated frequently performed activities, like locomotor behaviors, with anatomical variation [e.g., variation in the musculoskeletal anatomy of the shoulder girdle associated with different locomotor behaviors (Ashton and Oxnard, 1964)]. Those behaviors that have regularly been adopted in primate lineages are believed to have greatly influenced the overall diversity we now see across the Primate Order. Napier (1967) argued that phylogenetic history has driven postural and locomotor tendencies, and by association functional morphology, in different ways across different primate clades [postural: pronograde toward orthograde; locomotion: hindlimb-dominated locomotion (leaping) to quadrupedalism to forelimb-dominated locomotion (suspensory, climbing)].

Much of the recent research into primate locomotion and posture has focused on better understanding the role that both ecology and morphology play in the positional behaviors a primate may or may not be likely to adopt. McGraw (1996a) called this a “multivariate problem” influenced by a myriad of factors rooted both in the biological characteristics of the animal in question and the structural, behavioral, and ecological elements of its habitat. Garber (2007) divided these factors into three camps: physiological, ecological, and social/behavioral (Figure 1.1).
One of the most frequently cited influences on primate positional behavior is a primate’s body size. Based on an earlier study of seven platyrrhine monkey species from Surinam (Fleagle and Mittermeier, 1980), Fleagle (1985) argued that small-bodied primates, as a result of their inability to reach as far as their larger-bodied relatives, should need to leap more often to cross canopy gaps. Conversely, larger-bodied primates can cross these same gaps through potentially less risky bridging or climbing. Some studies have supported this association (e.g., Youlatos, 1999) while many others have not. Comparing six cercopithecoid species in the Tai Forest, Cote d’Ivore, McGraw (1998a) found no clear association between body size and frequency of leaping and an equivocal association between body size and climbing. Gebo and Chapman (1995a) found the opposite relationship observed by
Fleagle and Mittermeier (1980) with five cercopithecoid species in Kibale Forest, Uganda. In Kibale, the smaller-bodied primates leapt less often and climbed more often than did the larger sympatric primates. Among New World primates, Garber (1991) found no clear association between body weight and leaping or climbing for three tamarin species.

Other researchers have tried to identify trends in specific musculoskeletal morphologies that are tied directly to the biomechanics of positional behavior. For over a century, the intermembral index has been used as a measure of the proportional relationship between forelimbs and hindlimbs in primates (e.g., Mivart, 1873). Fleagle (1976) compared the skeletal morphology of two sympatric leaf monkeys with differing locomotor patterns. The animal that leapt most frequently exhibited a lower intermembral index (i.e., longer hindlimbs to forelimbs) while the more quadrupedal animal exhibited limbs of more similar length. Longer hindlimbs in leapers might be expected given the role that this limb plays in the propulsion and energy dissipation of leaps (Strasser, 1992). Similarly, researchers have associated long distal limb elements (i.e., forearms and legs) with increased terrestrial quadrupedalism and/or leaping (Rodman, 1979) and long forelimbs with suspensory locomotion (Cant et al., 2003). Other studies have looked directly at muscle mass differences in species for associations with locomotor behavior. Fleagle (1977) compared the relative muscle mass of two sympatric Malaysian leaf monkeys and found clear contrasts between the species that correlated with observed differences in leaping, quadrupedalism, and forelimb suspension.
Researchers can use results from these types of comparisons to generate biomechanical models that can then be tested directly under controlled conditions (e.g., laboratory-based radiography, strain gauge, and electromyography studies) (Fleagle 1979).

Today, primatologists in laboratory settings across the world are able to use a greater understanding of the underlying bone biology associated with primate biomechanics coupled with more sophisticated technologies to analyze primate locomotor/postural adaptations in even greater detail. As a result, many current form-function studies focus on identifying associations between the size and shape of finite elements of skeletal morphology [e.g., the degree of projection for a particular skeletal muscle anchor [see edited volume by Gebo (1993) for numerous examples] or bone microstructure [see Ruff and Runestad (1992) for an overview]. Given the growing endangered status of non-human primates, these studies have the advantage of deriving data directly from skeletal remains that are sometimes more accessible than live subjects. The results of these studies are also useful for reconstructing the behavior of extinct primates for whom soft tissue preservation is rare. It is through the combination of controlled experimental studies coupled with rigorous observational field techniques that we are better able to understand the behavioral correlates to modern primate morphological variation.

One area of growing interest is that role ontogeny plays in a primate’s willingness or capability to use certain positional behaviors. Both morphological differences between age groups (i.e., body size differences) as well as experience at
performing certain positional behaviors may restrict non-adult primates from exhibiting a pattern similar to their adult group-mates. Bezanson (2006) found that *Allouta palliata* young leapt significantly more often and bridged significantly less often than did adults. Similarly, Wells and Turnquist (2001) found that young Cayo Santiago Rhesus macaques (*Macaca mulatta*) exhibited a more varied pattern of positional behavior, with greater contributions of different locomotor and postural categories, than did adults. These age-based differences appear to be inconsistent between species. Bezanson (2006) found that *Cebus capucinus* only exhibited significant positional behavior differences at the most extreme age categories (adult vs. infant). Subtle postural and locomotor differences have also been observed between male and female primates and are typically attributed to contrasting social responsibilities, nutritional requirements, and/or body sizes (Gebo, 1992; Doran, 1993; Chatani, 2003).

We cannot assume that a primate’s positional behavior is merely a product of its morphology or physiology. Rather, morphology and physiology together underlie the strategies by which a primate meets multiple ecological and social challenges (e.g., finding and acquiring food, escaping potential predators, accessing mating opportunities, defending offspring). Therefore, a primate’s external environment is a critical influence on the postural and locomotor behaviors that are performed. Primates are largely an arboreal radiation with species spread across many ecologically distinct habitats (Napier, 1967). Living primates inhabit a variety of environments (e.g., savannas, rainforests, woodlands), navigate a variety of forest
strata, and utilize supports of differing sizes and orientations. Given this ecological diversity, contrasts in the use and nature of forest architecture have no doubt influenced the patterns of positional behavior that we observe in the wild and helped shape the morphological variation apparent throughout extant and extinct members of the Primate Order.

Locomotion and posture within an arboreal environment have been the focus of many hypotheses aimed at explaining modern primate behavioral variation (e.g., Napier, 1967; Fleagle, 1985; Cannon and Leighton, 1994). Primates negotiating arboreal supports face two significant challenges: balance and body mass support. As primate body mass increases, the proportion of all available supports capable of bearing their weight is predicted to decrease (Fleagle, 1985; Cant, 1992) Large-bodied, arboreal primates may restrict themselves to parts of the canopy where large supports are common (Youlatos, 1999), they may rely more heavily on suspensory locomotor patterns (Fleagle and Mittermeier, 1980) or they may employ postures and locomotor behaviors that distribute their body weight across numerous supports (Fontaine, 1990). Additionally, as limb length increases, a primate’s center of gravity moves further away from any support on which it chooses to stand and this may compromise its ability to balance (Rose, 1993). To maintain balance, primates may increase the flexion at the knees and elbows to bring their center of gravity closer to the support surface (Cant, 1992; Rose, 1993). In laboratory studies, Old World monkeys have been shown to crouch more when walking atop arboreal supports than when walking on the ground (Schmitt, 1999).
Both balance and weight support have been shown to play a significant role in a primate’s tendency to use certain types of supports and formed the based arguments explaining postural and locomotor patterns in certain species (e.g., Fontaine, 1992; Doran, 1993; McGraw 1998a,b; Youlatos, 1999).

Within an arboreal environment, a primate’s ability to cross breaks in the canopy has also played an important role in understanding primate positional behavior tendencies (Fleagle, 1985). Arboreal habitats are rarely homogeneous. As arboreal primates move between potential feeding/resting sites, they are likely to face numerous canopy gaps that cannot be crossed via quadrupedal locomotion (Cant, 1992). Given their different body sizes and morphologies, different primate species might be expected to use different strategies to cross canopy gaps. Cannon and Leighton (1994) noted that the frequency and size of canopy gaps play a significant role in predicting how a primate will navigate its arboreal habitat. The authors compared the positional behavior of long-tailed macaques (Macaca fascicularis) and Bornean agile gibbons (Hylobates agilis). They found that long-armed gibbons could cross wider canopy gaps, through both leaping and brachiation, and relied less heavily on thinner periphery canopy branches than did macaques. In contrast, the macaques were more restricted in the types of gaps crossed and relied on thinner supports more often near the periphery of tree crowns. Cannon and Leighton (1994) suggested that more generalized macaques must make their locomotor decisions (i.e., to leap or not to leap) by balancing the dangers imposed by leaps (i.e., falling), and the high energy demands of propulsive
leaping against the potential costs of less direct foraging (i.e., arriving at food patches after competitors). Cannon and Leighton (1994) argued that high rates of quadrupedalism and low rates of leaping and climbing in macaques in comparison to gibbons was likely a product of their rejection of a greater number of gap-crossing opportunities.

Primates choose to cross gaps for a number of reasons, including the acquisition of desired food items. Foraging is an important component of all wild primates’ daily activity patterns. In fact, Fleagle (1984) proposed that food location and acquisition is the most important factor governing primate positional behavior. Despite its proposed significance, Fleagle (1984) also found that diet and locomotor behaviors were poorly correlated with few similarities between primates broadly characterized as having a certain diet. For example, all frugivores are not more likely to leap than folivores or insectivores. Fleagle (1984) noted that one reason for the poor correlation between diet and locomotion is that primates with similar diets may use supports very differently to acquire broadly similar food types. Some primates may leap or bridge across forest gaps to enter nearby tree crowns to acquire fruits while others may climb to the ground and move terrestrially between tree trunks to acquire the same fruits.

While locomotor tendencies may not be associated with broad dietary categories, there is some evidence that posture is more closely associated with diet. Primatologists often use the concepts of spatial and temporal patchiness to describe different distributions of food types in a primate’s habitat (Oates, 1987). Patchiness
can include multiple variables including patch size, distance between patches, and temporal patchiness (i.e., seasonality). Food types preferred by different primate species may differ substantially in patchiness. Leaves, even less abundant young leaves, are seen as a somewhat ubiquitous, less patchy food resources in forest environments when compared to other food types such as ripe/unripe fruit and non-social insect prey (Garber, 1987). This is because leaves are typically found in large clumps, each tree produces many leaves, and trees maintain their leaves for a larger percentage of the year than either flowers or fruits (Oates, 1987). McGraw (1998) argued that the clumped nature of leaves allowed colobus in the Tai Forest, Cote d’Ivoire to move directly between clumps of leaves, feed on those clumps, and digest the leaves while resting for long periods between foraging bouts. This resulted in high frequencies of Sit (i.e., ischia and/or upper thigh resting on a support) and Lie (i.e., torso resting directly on a support) for the Tai colobus but low frequencies of Stand (i.e., weight balanced above a support on hands and/or feet). Conversely, guenons in the same forest exhibited more standing postures. These postures, McGraw (1998) argued, may have been associated with the patchier distribution of the guenon’s preferred food items (i.e., fruit and insects) in that they could spend less time feeding at each individual patch and they were forced to use postures that facilitated more active movement throughout the canopy. Standing postures allowed for a rapid transition to a variety of locomotor behaviors that might be needed to acquire highly competitive and, in the case of insects, mobile food resources.
Variability of Positional Behavior

Given the range of positional behavior decisions (e.g., choice of supports, arboreal routes, canopy heights) a primate makes each day and the various factors influencing a primate’s locomotor and postural profiles, it is reasonable to expect primate positional behavior to exhibit a high degree of intraspecific variation and individual plasticity. Given several hypothetical forests that differ in terms of forest architecture (e.g., frequency/size of canopy gaps, tree size, tree species density, substrate variability), we might expect the same primate species inhabiting each of those forests to adapt its available range of postures and locomotor categories to each specific forest habitat (Figure 1.2). In other words, if primate positional behavior is determined—even in part—by the structural (architectural) context of that behavior, then we ought to see changes in locomotion and posture of primates inhabiting structurally distinct forests.
Figure 1.2: Primate Positional Behavior Variation Across Habitats. Supposing one finds a single primate species distributed across structurally different habitats, this figure illustrates two alternate hypotheses affecting their postures and locomotor modes they might assume.

Of course, if positional behavior were found to be highly variable and heavily dependent upon forest architecture, this would present a seemingly insurmountable challenge to those interested in using primate morphology to infer positional behavior from the fossil remains of extinct primates. One goal of documenting the positional behavior of living primates is to identify predictable associations between
primate anatomy and patterns of posture and/or locomotion. Fleagle (1979) outlined a naturalistic approach to identifying these associations that stressed quantification of both musculoskeletal anatomy and observed patterns of positional behavior. Interspecific differences in positional behavior can then be compared to differences in musculoskeletal anatomy to propose hypothetical associations between the two that can be further tested and refined with the inclusion of more species. Once patterns are established, these morphological elements can be looked for in the remains of fossil primates and used to reconstruct their likely locomotor and/or postural behaviors. For example, Nakatsukasa (2004) reviewed his own and his colleagues’ work reconstructing the positional behavior of the Middle Miocene hominoid called *Nacholapithecus*. Using morphological similarities between *Nacholapithecus* and various living primate species, several researchers reviewed in Nakatsukasa (2004) and the author himself inferred that this ape was a slow-moving, orthograde climber that pre-dated the shift toward the suspensory behavior characterizing later hominoids. The accuracy of these types of reconstructions depends on reliable associations between living primate morphology and positional behavior. In other words, the appearance of a certain trait or set of traits can only be considered predictive of a positional behavior profile if those traits are reliably correlated with those positional behaviors whenever they are found in living primates.

Differentiating species-specific positional behavior from site-, seasonally-, or sex-specific positional behavior is necessary to identify consistent interspecific
trends in primate positional behavior [e.g., associations between anatomy and behavior that are characteristic of a species and capable of being compared to fossil anatomy (Dagosto and Gebo, 1998)]. Dagosto and Gebo (1998) urged caution when comparing positional behavior studies when they noted:

One may...believe that one is testing for a species’ effect, but in fact a number of other effects, including those from habitat structure, seasonal differences in behavior, interobserver ‘error,’ degree of habituation, presence and density of predators, age/sex composition of the groups, etc. could influence the result (p.17).

In other words, there are many factors unlikely to vary between forest habitats such as average adult female body size for a species, the physiological processes associated with digesting different food items, inherited morphological traits, or the general patchiness of foods classified into broad dietary categories (e.g., leaves vs. fruit). If these static factors drive primate positional behavior, we might assume that the positional behavior observed during one or several studies of a primate species is intrinsic to that species no matter the habitat. On the other hand, there are numerous factors (e.g., forest structure, predation risk, particular food species density, habitat disturbance) that are likely to vary between forests habitats. If these less static factors drive positional behavior, we might find comparing between species, for which we lack a clear species-specific positional behavior profile, far more difficult (Dagosto and Gebo, 1998). The challenge in authenticating proposed associations between morphology and certain positional behavior profiles lies in identifying which of these two broad categories of factors are driving patterns of positional behavior in living primates.
To address these criticisms, positional behavior researchers have created natural experiments aimed at testing the degree to which primates maintain positional behavior profiles across structurally distinct habitats (Doran and Hunt, 1994; Garber and Pruetz, 1995; Gebo and Chapman, 1995b; McGraw, 1996b). These experiments include sampling positional behaviors for one or more species spread across forests that differ structurally in some way. Typically, these experiments are conducted during equivalent times of year to avoid any confounding affects of seasonal differences and observations are restricted to individuals of the same age/sex classes. These experiments are based on two alternate hypotheses. If positional behavior remains conservative across variable habitats, the tight link between anatomy and positional behavior—and the behavioral inferences based on this association—is supported. If positional behavior varies greatly between distinct habitats, the environment is proposed to exert a substantial influence over primate positional behavior. This brings into question any behavioral inferences for extinct primates for whom we rarely know much about their ancient habitats.

To date, most studies have shown that the positional behavior of most wild primates is largely conservative (Table 1.1). In other words, most studies have shown that given a habitat in which a primate species can use its preferred locomotor or postural behaviors, it will choose to do so. Still, the presence of some evidence to the contrary is concerning. For example, while McGraw (1996a) found little evidence of positional behavior variation for C. badius, Gebo and Chapman (1995b) found that the red colobus did exhibit differing positional behavior patterns
between seasons, years, and habitats. This contrast between studies highlights several important questions. Are these studies really looking at the same phenomena and asking the same questions? In other words, are these authors drawing different conclusions about similar data or are their approaches influencing their interpretations? Methodological concerns were discussed at length by Dagosto and Gebo (1998) and have led to numerous refinements in positional behavior research design (several of these are discussed in chapter 4). However, it is possible that differing results between studies might not rest in methodology as much as in interpretation. At what point do behavioral changes threaten established form-function associations? The implications of either declaring positional behavior conservative (i.e., strongly regulated by evolutionary history) or plastic (i.e., influenced by variable external factors) are profound if they cause us to doubt the close association between morphology and behavior in living, and by extension extinct, primates.
<table>
<thead>
<tr>
<th>Species</th>
<th>Positional Behavior Differed</th>
<th>Positional Behavior was Conserved</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moustached Tamarin (Sanguinus mystax)</td>
<td></td>
<td>√</td>
<td>Garber and Pruetz, 1995</td>
</tr>
<tr>
<td>Western Red Colobus (Colobus badius)</td>
<td>√</td>
<td>√</td>
<td>Gebo and Chapman, 1995b; McGraw, 1996b</td>
</tr>
<tr>
<td>King Colobus (Colobus polykomos)</td>
<td></td>
<td>√</td>
<td>McGraw, 1996b</td>
</tr>
<tr>
<td>Olive Colobus (Colobus verus)</td>
<td></td>
<td>√</td>
<td>McGraw, 1996b</td>
</tr>
<tr>
<td>Campbell’s Monkey (Cercopithecus campbelli)</td>
<td></td>
<td>√</td>
<td>McGraw, 1996b</td>
</tr>
<tr>
<td>Diana Monkey (Cercopithecus diana)</td>
<td></td>
<td>√</td>
<td>McGraw, 1996b</td>
</tr>
<tr>
<td>Chimpanzee (Pan troglodytes)</td>
<td></td>
<td>√</td>
<td>Doran and Hunt, 1994</td>
</tr>
</tbody>
</table>

Table 1.1: Results of Intraspecific Studies of Positional Behavior. This table shows the results of intraspecific studies comparing groups of seven primate species by single researchers using the same methods in structurally distinct habitats and their results.

McGraw (1996a) suggested that it may be less of a question of whether positional behavior differs between forest habitats but rather how different must habitats be to produce that difference. For example, primates adapted to below-branch swinging are likely to use that strategy if a reasonable arboreal pathway exists. If the same individuals were to be placed in an environment where such a locomotor strategy is impossible or of no usefulness, then there would be no reasonable expectation for them to try to use it. Thus, the question becomes a matter of degree.

In this study, I compare neighboring primate groups ranging across a forest fragment at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana that is characterized by varying degrees of anthropogenic disturbance. Two groups of each species were selected for their degree of habituation and the degree of forest disturbance.
disturbance within their range. I followed each group over a 10-month observational period and recorded categorical data on daily activity patterns for adults of each species. I describe these species, the site and types of habitat disturbance in chapter 2 and compare forest structure using several ecological sampling methods in chapter 3. Using these ecological differences as context, I test for differences in forest strata and support usage (chapter 5), posture (chapter 6), and locomotion (chapter 7). In chapter 8, I examine positional behavior variation from another angle and compare patterns of positional behavior for each group by sex. I conclude (chapter 9) by presenting overall species’ postural and locomotor profiles at BFMS, summarizing the findings of this project, and comparing them to a study of positional behavior conducted on closely related living species as a test of interspecific consistency in primate positional behavior.
Chapter 2: Boabeng-Fiema Monkey Sanctuary

Chapter Overview

In this chapter, I provide the ecological context for this study. I briefly describe the history, climate and ecology of Boabeng-Fiema Monkey Sanctuary (BFMS), and introduce what is known about the behavioral patterns of the two dominant monkey species found within the sanctuary. Finally, I discuss the complex interface between monkey and human populations located within and around the sanctuary. These factors are interwoven to produce the unique socio-ecological setting for my study populations and are essential for understanding the nature of the forest-monkey-village interrelationship at BFMS.

The Boabeng-Fiema Monkey Sanctuary

BFMS is a small, locally managed and protected forest habitat in central Ghana, West Africa. The sanctuary is located at 350m above sea level in the Brong-Ahafo region and is surrounded by several local villages, notably the smaller village of Boabeng bordering the sanctuary to its eastern edge and the larger village of Fiema to the northeast (Figure 2.1). The forest habitat at BFMS is part of a complex forest system (192ha) connected to smaller surrounding forest fragments (ranging in size from 54.1–3.2ha) by roads, agricultural land and tree corridors of varying
Figure 2.1: Map of Ghana and BFMS. The location of Ghana’s Boabeng-Fiema Monkey Sanctuary. The inset shows a map of the sanctuary including dirt roads; trail systems, and the western border of the village of Boabeng. In addition, the inset shows areas of forest regenerating from past use as farmland and mixed disturbed forest comprised of edge effects, small forest clearings and thin primary tree corridors.
density (Wong and Sicotte, 2006). Fargey (1992) described the forest at BFMS as dry semi-deciduous with a “sparse tree understory” separated by a transitional zone of closed woodland forest from surrounding derived savannah. This study focuses on those primate groups inhabiting what Fargey (1992) called the dry semi-deciduous and closed woodland forest west and south of the village of Boabeng and does not include primates living in the surrounding savannah zones.

Like much of Ghana, BFMS is characterized by two distinct rainy and dry seasons. Fargey (1992) reports that the area around Boabeng-Fiema experienced 1250mm mean rainfall from 1985–1990 with the heaviest rainfall occurring between March and October (peak rainfall in June and September). Saj et al. (2005) recorded a slightly lower rainfall total of 1049.5mm between August, 2000 and July, 2001. In conversation with locals during this study, the dry seasons were typically described as running from December to March with a shorter period between July and August. The longer period occurs early in the year and is notable for the dry air that blows down from the north (Harmitan), leaving a thick patina of red dirt covering vegetation and structures. The wet period was often described as running from March to July and September to November with an expectation for the heaviest rains in June and September.
**Recent Forest Research**

Recent researchers have described the forest at BFMS as a “mosaic” that includes areas of unlogged primary forest, regenerating farmland, disturbed forest edges, and woodland areas dominated by savannah tree species around the periphery (e.g., Saj et al., 2005). In addition to areas of forest regeneration, remnants of past agricultural use in and around the forest sanctuary include the presence of non-native trees including teaks, cocoa, mango, and various citrus trees, as well as trail systems leading through the sanctuary to surrounding community farms.

Of the two areas included in this study, the forest area bordering the village of Boabeng to the west is least disturbed with a tall, mostly interconnected canopy and minimal evidence of past clearing. Saj et al. (2005) reported the results of an ecological survey of BFMS consisting of nine randomly placed 50m by 50m plots. The authors found that this unlogged area of the forest exhibited greater average tree species diversity (20.8 per plot), intermediate average tree density (50.4 trees per plot), and intermediate tree species diameter at breast height (31.6 cm DBH) compared to more disturbed forest areas. Fargey (1992) also noted that 25% of the trees in this area were larger than 40m in height, though it is unclear what criteria he used to exclude smaller or immature trees. The unlogged forest continues to be highly valued by the local ecotourism enterprise and is targeted heavily by continued conservation efforts (pers. observ.).

South and southwest of Boabeng, the forest is more heterogeneous with wide gaps in the canopy. Alternating patches of regenerating farmland with limited
groundcover and thick forest with an extremely dense substrate cover this area. Saj et al. (2005) noted that the areas of regenerating farmland in this region exhibited the highest average DBH (40cm) but fewest trees per plot (13.5 avg.), likely as a result of selective land clearing.

The forest bordering the edge of the village of Boabeng, along a narrow corridor to the west, and a much wider corridor to the south, is highly disturbed. This edge forest is a mix of areas of extremely dense understory, short trees, and high levels of human-monkey interaction. Saj et al. (2005) found that this area exhibited the smallest average DBH (28.1cm) and a high proportion (22% of trees surveyed along edge) of a single tree species (*Grewia mollis*) characteristic of disturbed forests.

*Monkeys at BFMS*

Two primate species are found in large numbers within BFMS: the ursine colobus (*Colobus vellerosus*) and Lowe’s monkey (*Cercopithecus campbelli lowei*). These species are referred to locally as the “black-and-white” and “mona” respectively. In Figure 2.2, I summarize the behavioral traits of these species and review literature concerning these species below.
Figure 2.2: Species Portraits. These portraits summarize general characteristics of the two predominant monkey species found at BFMS. These facts are summarized from the behavioral data presented below. Group sizes were derived from personal field observations. Average body weights were derived from data collated and published by Delson et al. (2000).
Species 1: *C. vellerosus*

*C. vellerosus*, or the ursine colobus, is a more recently recognized colobus species of the black-and-white colobus clade from the cercopithecoid subfamily Colobinae (Grubb et al., 2003). Since 2000, researchers from the University of Calgary have gathered much data on the social behavior, foraging strategies, and population structure of this species at BFMS (see references below).

The diet of *C. vellerosus* can be considered predominately folivorous. Saj et al. (2005) reported that *C. vellerosus* at BFMS subsisted on a large proportion of leaves (79%) with smaller proportions of fruits/seeds (11%), flowers (6%), and seedpods (4%). Further, Saj and Sicotte (2007a) reported that folivory increased dramatically (84-100%) during July and August when other food resources were not available. Overall, Saj and Sicotte (2007a) characterized *C. vellerosus* as a primate that feeds on a diverse variety of tree species, distributed widely across their range (i.e., unclumped), and found within large enough canopies to meet the dietary needs of each group member (i.e., low intragroup feeding competition). *C. vellerosus* foraging strategies may be influenced more by group size than resource distribution. Saj and Sicotte (2007b) argued that larger *C. vellerosus* groups increased their day range to meet the greater overall dietary needs of the group, and that females in larger groups may have increased their distance between other group members and/or reduced the number of neighboring feeders.

Another topic covered in detail by researchers at BFMS is the nature of intergroup aggression and intragroup affiliation. Encounters between *C. vellerosus*
groups at BFMS are frequent and tend to involve male aggression directed at individuals of either sex and are thought to reflect either advertisements of personal fitness (i.e., to increase mating opportunities) and/or attempts to defend mates within one's own group (i.e., prevent extragroup copulations) (Sicotte and Macintosh, 2004). In contrast, male takeovers or attempts at takeover tend to target females and their infants (Sicotte and Macintosh, 2004). During a 13-month study between 2004 and 2005, researchers reported several cases of confirmed (n=3) and suspected (n=4) infanticide for *C. vellerosus* at BFMS and a high rate of overall infant mortality due to infanticide (71.4%) (Teichroeb and Sicotte, 2008). These infanticide events involved male infants more often than females and tended to be carried out by males achieving high rank by taking over new groups or lower ranking males that were part of all-male bands (Teichroeb and Sicotte, 2008).

Current research suggests that high infanticide rates have a profound influence over other types of colobus behavior at BFMS. Though female *C. vellerosus* disperse (at least occasionally) from their natal groups at BFMS, females may form coalitions, reinforced through affiliative behaviors (i.e., grooming), to fend off infanticide attempts by males (Saj et al., 2007). Alternately, females may direct affiliative behaviors (i.e., grooming bouts) at males to increase the likelihood that males will defend their infants even after they have lost group dominance (Saj and Sicotte, 2005; Saj et al., 2007). The significance of infanticide is further inferred from the high degree of vigilance exhibited by *C. vellerosus*, particularly during intergroup encounters or in areas of their home range that overlap with other colobus groups
(Macintosh and Sicotte 2009). Whether infanticide and infanticide-associated behaviors are an evolutionarily selected male reproductive strategy in this species or a response to anthropogenic habitat disturbance at BFMS remains unclear.

The forest sanctuary at BFMS is connected to surrounding populated but less well-protected forest fragments. *C. vellerosus* populations in the sanctuary and these surrounding smaller fragments have exhibited a complex pattern of population growth. Using data from an unpublished census in 1991 and another conducted by the authors in 2003, Wong and Sicotte (2006) showed that the population size of *C. vellerosus* at BFMS increased by 78.9% and the number of individual groups doubled. Further, the authors found that the *C. vellerosus* population increased an additional 14.5% between 2000 and 2003, reaching a total of 15 separate groups and 217–241 individuals. Wong and Sicotte (2006) also censused the *C. vellerosus* populations found in three surrounding forest fragments and identified an additional six groups with a total population of 58–61 individuals. When the authors compared these findings to an earlier 1997 unpublished census they argued that the surrounding fragment populations have remained largely stable over time (one increasing, one decreasing, and one unchanged). The increase in population size within the sanctuary at BFMS, compared to the surrounding communities may be the result of immigration from smaller nearby forest fragments with fewer food resources (Wong and Sicotte, 2006).
Species 2: *C. campbelli lowei*

*C. campbelli lowei* or Lowe’s monkey is a member of the *Cercopithecus* genus. Grubb et al. (2003) associated *C. campbelli lowei* with the mona group of the *Cercopithecus* genus. *Other* taxonomists have considered *C. lowei* a full species and separated it from its traditional sister subspecies *C. campbelli campbelli* (Groves, 2001).

In comparison to *C. vellerosus*, there is very little published data on the socioecology of *C. campbelli lowei*. Using the locally preferred term “mona monkey,” Fargey (1992) noted that *C. campbelli lowei* “primarily feeds on fruits, young leaf shoots and insects” (p. 155). It is unclear whether this was the author’s personal observation or derived from other studies of “mona monkeys.” The use of detailed dietary studies of *C. campbelli lowei*’s sister subspecies may be more informative. *C. campbelli* or Campbell’s monkey has been studied extensively in the Tai Forest of Cote d’ Ivoire. Between 2000 and 2001, Buzzard (2006) recorded a diet for *C. campbelli* comprised of 46% fruits, 8% foliage, 33% animal prey, 1% flowers, 2% fungi with the remaining 10% consisting of either cheek pouch feeding where the food type was not identifiable or other food sources.

While the preponderance of fruit and animal, particularly insect, prey in the diet of *C. campbelli* matches my own observations of the *C. campbelli lowei* diet at BFMS, caution should be taken in equating Tai and BFMS guenon groups. First, precise data on food types consumed were not collected during this study for several reasons. Impassible sections of the forest and dense impenetrable vine
tangles near the ground prevented me from examining diet in detail (Figure 2.3). Additionally, since monkeys acquired both small fruits and insect prey or larva using both rapid hand movements and extensive manipulation of foliage, distinguishing between these foods was difficult. Second, *C. campbelli lowei* at BFMS depended heavily on the villages surrounding BFMS for food resources. Fargey (1992) observed that *C. campbelli lowei* frequently foraged for yam and cassava peels in the garbage heaps near the village edge. This was a daily activity during the course of my study. No doubt, this additional dietary resource influenced the overall intake of food resources from elsewhere in the guenon’s range.

![Image](image.jpg)

**Figure 2.3: Guenon Scanning Surrounding Supports and Foliage in Dense Understory.** Understory density throughout BFMS obscured close observation of guenons feeding there.
There are no published census data on *C. campbelli lowei* at BFMS and no census was conducted during this study. Fargey (1992) estimated that 216 *C. campbelli lowei* lived within the sanctuary in 1990. Today, local guides often tell visitors that approximately 500 *C. campbelli lowei* live in the sanctuary. This estimate may derive from a previous unpublished census but its accuracy is unclear and different individuals associated with sanctuary frequently offer alternative and widely divergent estimates. Whatever the total population, group density near the village is clearly quite high. In this study, two pairs of adjacent groups were followed in two different forest areas for a total of 4 separate guenon groups (see chapter 3 for a description of group ranges). The home ranges of each group in these pairs overlapped. In addition, each group was surrounded by additional groups with whom contact was frequent.

**Other Fauna at BFMS**

There have been rumors of other primate species living inside or immediately around BFMS including Diana monkeys (*Cercopithecus diana*), spotted guenons (*Cercopithecus petaurista*), patas monkeys (*Erythrocebus patas*), and green monkeys (*Chlorocebus sabaesus*). Recent researchers do not report seeing these species within the sanctuary, however, Saj et al. (2006) did report the presence of a single olive colobus (*Procolobus verus*) and sightings of the galago (*Galago senegalensis*) at BFMS. Throughout the study, farmers and foreign volunteers from surrounding communities often described monkeys to me that
could easily have been any of the rumored species. On two occasions, I witnessed juvenile monkeys, likely young patas monkeys, being kept as pets in nearby villages.

The greater cane rat (*Thryonomys swinderianus*), known locally as the "grasscutter," was often talked about and eaten in the communities surrounding BFMS. While I never observed a living specimen within the sanctuary, locals explained the holes dug by children in the forest as evidence of attempts to find "grasscutter" young. The hammer-headed fruit bat (*Hypsignathus monstrosus*), squirrel (*Funisciurus* sp.), and a species of mongoose were regularly seen throughout the forest. Other wild fauna included various bird, snake, lizard, and invertebrate species. Domesticated fowl (guinea fowl, chickens, and ducks), sheep, and pigs often traveled and foraged throughout the forest (Figure 2.4). Both dogs and goats were restricted from entering the forest due to the perceived threat they pose to the local monkey population and their ownership was prohibited in the villages near BFMS.

![Domesticated Animals at BFMS](image)

**Figure 2.4: Domesticated Animals at BFMS.** These photos show a sheep and chickens foraging along the edge of trails and roads within the sanctuary. Additionally, pigs and other domesticated fowl regularly traveled, foraged, and rested within the forest bordering the village of Boabeng.
Predation risks for the two primate study species are likely low at BFMS. Macintosh and Sicotte (2009) found that vigilance behavior exhibited by *C. vellerosus* increased as they moved to lower heights in the canopy, a trait common in animals with significant predation threats from terrestrial sources. However, the authors noted that the crowned eagle (*Stephanoaetus coronatus*) is the only potential predator of *C. vellerosus* at BFMS and most locals regarded the possibility of predation as unlikely. While predation risks for *C. campbelli lowei* are likely similar to those for *C. vellerosus*, on three separate occasions I witnessed groups of *C. campbelli lowei* climb into the branches above large-bodied snakes on the forest floor and vocalize repeatedly for up to half an hour. I never witnessed similarly strong reactions by *C. vellerosus* to any potential predators.

**History of BFMS: Taboos and Conservation**

Surrounded by several largely agricultural villages, BFMS is notable as a nexus of human and nonhuman primate interaction. Throughout its history, both the human and nonhuman primate communities at BFMS have relied heavily on the local ecosystem for their natural resources (Saj et al., 2006). Through a complex interweaving of local traditions, historical events, and conservation practices, a mutual dependence on the forest habitat has blossomed into a form of interdependence.

Saj et al. (2006) documented the evolution of BFMS from a locally grown conservation strategy into an ecotourism enterprise. Local traditions in the
communities surrounding the sanctuary have historically promoted a spiritual
association between the monkeys and two prominent deities. Each deity is
associated with one of the larger surrounding villages (Boabeng and Fiema) and one
of the native monkey species (*C. campbelli lowei* and *C. vellerosus*). Respect and
rituals associated with these deities have translated into a community-wide cultural
obligation to protect both monkey species (Figure 2.5). This obligation is enforced
by community elders, notably the fetish priests of each village, and includes a
prohibition against hunting or harming either species. The local hunting taboo is
reinforced through stories of terrible misfortunes (often illness or death) befalling
those who violate it. The historical depth of this tradition is unclear, however and
Saj et al. (2006) noted that aspects of the myths underlying it may have changed to
reflect the growing importance of foreign tourists.
The spiritual association between the communities and the local monkey populations has not always gone unchallenged. In the 1970s, a Christian sect tested the power of the native deities by violating the taboo and hunting the monkeys at BFMS (Fargey 1992; Saj et al. 2006). As a result, through Ghana’s Department of Game and Wildlife, the local taboo was codified into a law preventing the killing of all monkeys within an established 4.8 km radius (Fargey 1992). Today, the local community members describe these events as resulting in a rift within the local villages and the establishment of two new satellite human settlements. The precise
effects of this violation are unclear, though oral history suggests that the size of the monkey population at BFMS may have diminished dramatically during this time (Saj et al., 2006).

Today, ecotourism at BFMS has become a consistent source of revenue for the local economy (Saj et al., 2006; Figure 2.6). Tourists include foreigners, large Ghanaian school groups, and smaller organizations or families visiting from areas throughout the country. During the course of this study, tourists visited the site nearly every day though there were fluctuations in the frequency and size of tourist groups. Ecotourism at the sanctuary is governed through the cooperation of the local BFMS Management Committee, comprised of representatives from many of the surrounding communities, and the Wildlife Division of Ghana’s Forestry Commission. Throughout 2010, there was much debate regarding the governance of the sanctuary and it appeared that by the end of this study, much of the management of and revenue from BFMS was going to be placed under local control.

Local villagers are employed by the BFMS Management Committee and provide tours of the entire sanctuary or tours dedicated to observing certain monkey activities (i.e., late afternoon raids on the village). A recently refurbished guesthouse that sits adjacent to the western end of the sanctuary provides accommodation for overnight visitors. A local couple from one of the surrounding communities runs the guesthouse and provides various opportunities for the employment (e.g., refilling water tanks, remodeling the facilities, maintaining the lawn, cleaning rooms, etc.) of other community members. Possible future
construction projects associated with this ecotourism enterprise include paving the local dirt roads, the construction of an internet café and restaurant, and the establishment of a high-end resort.

Figure 2.6: Ecotourism Attractions. Signs and markers such as this are found throughout the forest and are linked to local brochures describing medicinal uses for many of the local tree species.
**Interdependence and the Human-Monkey Interface at BFMS**

The historical taboo against hunting or harming the monkeys at BFMS remained strong during this project. From January to November 2010, I rarely witnessed aggressive interactions by the villagers against the monkeys. Within the forest, examples of human aggression against the monkeys typically included verbal threats, tossing rocks or dirt near the monkeys, or swinging sticks against low-hanging branches. These acts were almost always committed by children. The use of young children as a deterrent to crop raiding by monkeys is not uncommon in Africa as older children are often at school and adults are tied to farms or household chores (Chism, 2005). At BFMS, however, efforts to discourage this behavior were common. When observed by adults, these children were typically chastised, often harshly.

Rituals that associate the forest and the villages continue to reinforce the spiritual significance of the sanctuary. During this study, I was invited by community elders in Boabeng to observe an offering made at a sacred shrine located in the forest, as well as to attend a yam festival that included ritual offerings to one of the local deities at the home of Boabeng’s fetish priest. The fetish-priest’s role as a protector of the local forest was clear throughout my time at BFMS. For example, when a severely injured monkey was found in the forest, it was brought to the home of the fetish-priest to be watched until it died. He, along with the local chief and elder council, were regularly consulted regarding any activities that might harm or influence the monkey population. The connection between fetish-priest and monkey
extends even beyond death as indicated by a continually used cemetery (see Figure 2.5) within the sanctuary where both fetish priests and monkeys are buried together.

The possibility of increased revenue through ecotourism reinforces these traditions and creates an interdependence between the monkeys and human populations at BFMS. On one hand, villagers depend on the long-term health and accessibility of the primate species to realize the potential profits of their conservation investments. On the other hand, the primates depend on the local human population to protect their ecosystem and, increasingly, to provide supplementary food/mineral resources. This interdependence is not unusual in communities where human and non-human primates live in close proximity and is becoming an important issue in both primate conservation and primate socioecology [see Commensalism and Conflict: The Human-Primate by Patterson et al. (2005) for numerous case studies dealing with issues of monkey-human coexistence].

From conversations with local tour guides and visiting tourists, it was clear that the monkeys were the primary attraction at BFMS. While some attempt has been made to highlight alternate attractions (e.g., discussion about creating botanical or cultural tours), the significance of the colobus and guenon species to the success of the sanctuary is reinforced through the sanctuary’s name, souvenirs, and advertisements. Through surveys, Fuentes et al. (2007) found that visitors to the macaque tourist sites at Padangtegal, Sangeh, Alas Kedaton in Bali, Indonesia and in
sites at Gibraltar highly desired a “nature experience” that included viewing and interacting with monkey species. Visitors to BFMS often expressed similar desires. Viewing and interacting with both native species in a “natural” environment at BFMS is facilitated through the maintenance of an extensive trail system, prohibitions against littering, the establishment of several trash receptacles throughout the forest, tourist signage, and the habituation of the monkeys to human observation. Though officers from the Wildlife Division were stationed in Boabeng, the community and the tour guides regulated the day-to-day affairs in the forest by policing illegal or inappropriate activities and clearing trails. Meeting the demands of tourists not only contributes to the community through official revenue (i.e., tour fees, accommodation, etc.), but also supports individual community members through tips, souvenirs, small-scale vendors, and other tourism-associated activities.

Just as the village is dependent on the monkeys at BFMS, so too are the primates dependent upon the village and villagers. To differing degrees, all monkey groups studied exploited resources found within the village of Boabeng (Figure 2.7). *C. campbelli lowei* traveled into the village at least once a day and typically twice or more. The guenons gathered discarded food from refuse dumps, foraged around latrines, climbed into homes to steal prepared foods, gathered food items left out in the open, and raided storehouses. Furthermore, groups of *C. campbelli lowei*, particularly those in the areas of the forest with the heaviest tourist traffic, were often fed by tour guides and tour groups. Though discouraged by researchers, locals argued that this was a highly desirable activity for tourists, was little different than
monkeys scavenging for human food on their own, and netted higher tips. In contrast, *C. vellerosus* entered the village much less frequently. Typically once or twice during five-day observation periods, the colobus would feed on the leaves of trees isolated from the forest edge or lick/eat minerals from the side of mud brick buildings.

**Figure 2.7: Village Raiding.** These photos depict colobus and guenons visiting the village of Boabeng. The image on the left shows a group of colobus huddled along the exterior wall of a village home. At least once a week, colobus would cautiously enter the village to feed on village trees or, more often, to lick/consume minerals from village walls. The image on the right shows a young guenon scavenging from a mango pit disposed of along the village’s western edge. Several times a day, guenons raided the village in search of food contained in storehouses, disposed of in trash heaps, or placed near cooking preparation areas.
Conflict and the Human-Monkey Interface at BFMS

Despite the interdependence of human and non-human primate communities at BFMS, there are some potential conflicts that arise at this human-monkey interface. Crop raiding is an activity that pits the needs of non-human primates against human agriculturalists. Surveys reveal that small-scale agriculturalists living in close proximity to non-human primates often stress the negative economic impacts of primate crop-raiding (e.g., Newmark et al., 1994; Saj et al., 2001). For example, farmers living near vervet monkeys in Entebbe, Uganda reported losses they attributed to primate raiding at between $30 and $80 per month and up to $400 over a growing season (Saj et al., 2001). Proximity of agricultural fields to forest habitats, the type of crops grown, and the population density of the human communities being raided are all factors influencing the likelihood and extent of primate raiding behaviors. While direct crop-raiding may occur in the agricultural fields surrounding BFMS, raids of the storehouses, cooking areas, and households along the village border are a potential sources of conflict between C. campbelli lowei groups and the villagers of Boabeng. All guenon groups under study raided the village at least once each day. For the groups to the west of the village, food raids consisted of adults moving along roofs and the tops of tall walls surrounding central courtyards, traveling through the streets, and/or attempting to break into locked permanent agricultural storage sheds. Guenon study groups south of the village participated in all these activities but focused most of their raiding on refuse discarded in two waste dumps located along the forest edge. The significance of
these food resources can be inferred from the frequency with which aggressive intergroup territorial conflicts occurred at or near the village edge during this study. These conflicts typically entailed a series of chases, carried out primarily by females, until one group moved outside of a mutually claimed forest patch. 76% of all observed aggressive intergroup encounters (22 out of 29) occurred along the village edge or along the nearest trail parallel to the village edge.

Lee and Priston (2005) examined how primate activities such as crop-raiding may influence the attitudes and tolerance of neighboring human populations. The authors noted that human perceptions of primates are colored by their preconceived notions regarding primates (i.e., the cosmological relationship between human and non-human primates), the perceived impact of primate activities on the well-being of the human communities, and the economic realities surrounding primate-associated crop loss, such as the availability of government reimbursement programs. For example, Lee and Priston (2005) noted that when primates are viewed as “intelligent, vindictive and malicious—causing damage for the sake of damage” or when there are economic incentives for emphasizing primate roles in agricultural loss, their exploitation of human agricultural resources is perceived more negatively. These perceptions may be tempered and crop-raiding activities more tolerated when surrounding human cultures ascribe a spiritual significance to the monkeys.

At BFMS, the historic and supernatural connection between the monkey populations and the villagers coupled with the prospect of ecotourism income
clearly buffers the local primate community from negative perceptions. Saj et al. (2005) noted that villagers in Boabeng often watched and were entertained by *C. vellerosus* as they entered the village and during play. Additionally, the authors noted past surveys that have suggested a high regard for the cultural significance of the monkeys and a strong desire to maintain the monkey population. I noted a similar regard for both *C. vellerosus* and *C. campbelli lowei*. Villagers would often sit and watch the monkeys as they traveled along trails between the villages and surrounding farms. Even when the monkeys raided the village, locals would more often ignore them or sit and watch them rather than direct harm toward them.

Of all the interactions between monkeys and villagers at BFMS, village raiding by *C. campbelli lowei* was the most likely to result in human aggression towards the monkeys. During raids, the guenons would often pull boards off of permanent storehouses or reach through small openings to grasp stored maize. I also observed them on several occasions stealthily approach and then rapidly grab a piece of yam or cassava placed on the ground in preparation for cooking. Locals tolerated these small but regular raids except during times of food scarcity. From March–May mangos are in such high abundance in the village that many are discarded uneaten or directly offered to *C. campbelli lowei*. As this time of abundance came to a close, guenons shifted their raiding focus from mangos to maize. Numerous farmers commented that following a particularly poor growing season for maize, monkey raids were taxing an already limited food supply. Though
only anecdotally recorded in a daily follow diary, guenon raids at this time were more actively discouraged by shouts and rocks than during other times of the year.

The regard for monkeys at BFMS may not necessarily translate into increased protection for the forest. Saj et al. (2006) stated:

At the extreme, ‘caring for the monkeys’ could mean maintaining a few trees and providing provisioning. It seems that from the villager’s perspective the forest is not important for the survival of the monkey. This perspective can be traced back to the oracle’s instructions to take care of the monkeys themselves. These instructions have effectively focused on the bond between the humans and monkeys, and have not fostered stewardship of the forest for the monkeys. We frequently heard villagers say that if the villages were to move, the monkeys would follow. (p. 306)

While I heard similar statements including the belief that the monkeys would simply move into the homes of the villagers should the forest disappear, there is a greater recognition of the forest’s importance to the monkeys than these anecdotes suggest. For example, a Ghanaian NGO known as the National Conservation Research Centre (NCRC) has also become directly involved with BFMS and regularly sends representatives to survey the villagers on their reaction to conservation strategies. They have also initiated a program targeting a greater awareness of local conservation by training locals to go back to their own community and spread a general message of conservation as a non-outsider. Nevertheless, the increasing prevalence of land-clearing bush fires near the sanctuary, large patches of cleared forest outside of the sanctuary for the introduction of power lines in 2001, and the doubling of households in the local villages between 1968 and 1990 illustrate the potential threats to the continued survival of these monkey populations (Saj et al., 2005).
**Affects on Forest Architecture: Anthropogenic Habitat Disturbance**

In addition to direct competition over resources, other less direct conflicts threaten the stability of the human-monkey interface at BFMS. Some level of anthropogenic habitat disturbance can be perceived as a natural outgrowth of any situation in which small-scale agriculturalists live in close proximity to forest habitats. Marsh (2003) noted that deforestation, even on a small, localized scale, poses an important threat to primate populations for a number of reasons. Deforestation often results in fragmented forest systems in which individual fragments may not be large enough to meet the needs of remaining primate communities. It may also produce fragment edges containing plant species to which primates are poorly adapted. Following deforestation events, the matrix between fragments (e.g., cleared agricultural land) may limit migration and gene flow between populations. Marsh (2003) further noted that even after surviving fragmentation, primate communities are often faced with additional human pressures via hunting and the collection of forest resources.

The effects of anthropogenic habitat disturbance can be staggering. For example, Chapman et al. (2003) compared censuses of primate communities in forest fragments neighboring Kibale National Park, Uganda that they collected in 1995 to censuses collected in 2000. The authors attributed a 30% reduction in populations of black-and-white colobus and a 19% reduction in fragmented forest area capable of supporting primates to intensive use of the forest by neighboring
humans for fuel, charcoal production, gin distillation, beer brewing, and animal grazing.

BFMS is part of a larger fragmented forest system (Wong and Sicotte, 2006) and the sanctuary is heavily utilized by neighboring villages. Throughout the study, villagers regularly gathered firewood from the forest and collected other forest resources to produce traditional medicines or foods (see a complete list of trees and medicinal uses in Saj et al., 2005). The density of the forest understory often required that locals use cutlasses to cut personal trails through the forest. The larger, permanent trails were regularly cleared for use by both villagers and tourists, and it was not uncommon to see small vehicles (motorcycles, tractors, etc.) traveling along these paths. Large dumps, latrines, and pig sheds were kept along the village edge and many households used the edge of the forest as both a latrine and a dump. As stated earlier, the forest also served as a grazing area for domesticated sheep, pigs and fowl. Combined, these factors have produced a forest habitat that is highly altered and that places monkeys and humans at BFMS in close contact.

**Conclusion**

The presence of several well-habituated groups at BFMS distributed across areas of forest characterized by differing degrees of anthropogenic disturbance make it this site an ideal location to test the plasticity of primate positional behavior. Differences in the historical uses of parts of the modern sanctuary as either
farmland or sacred sanctuary have produced an uneven distribution of habitat
disturbance that will be discussed in detail in the following chapter. As noted earlier,
the forest west of the village of Boabeng is least disturbed and is the focus of the
ecotourism efforts at BFMS, while the forest south of the village, though protected,
exhibits much more habitat heterogeneity. Groups of both *C. vellerosus* and *C.
campbelli lowei* inhabit both the southern and western forests at BFMS (see Chapter
3 for description of study groups and their ranges). In subsequent chapters, I test for
intraspecific variation in positional behavior for colobus and guenons inhabiting
these forests.
Chapter 3: Forest Differences and Study Groups

Disturbed vs. Undisturbed Forests

In chapter 2, I noted several examples of anthropogenic disturbance at BFMS (e.g., human population growth, economic and social development projects, past use of the forest as farmland, current use of the forest for transportation, animal grazing, and resource acquisition). This disturbance has resulted in the “mosaic” forest structure observed by previous researchers (e.g., Saj et al., 2005) and described in detail in this chapter. To compare positional behavior in different forests, I required two habitats that were structurally distinct enough to be capable of producing the variation for which I was testing. In order to minimize confounding affects of phylogeny, primate groups of the same species had to inhabit these different forests. BFMS met both these requirements and proved to be an ideal site to conduct this study.

Forest disturbance at BFMS is not distributed evenly throughout the sanctuary. Instead, anthropogenic disturbance appears to be the product of a local compromise between the subsistence opportunities offered by clearing the forest, the cultural/spiritual significance of the forest to neighboring human communities, and the potential for profit promised through the growing ecotourism industry (see Chapter 2). As a result of this compromise, the forest west of the village of Boabeng,
once the site of most forest/monkey-associated rituals, has become the focus of modern ecotourism. This part of the sanctuary is often referred to locally as the “core” forest. Tourists are brought here to see well-habituated monkey groups as well as the tall canopy with its large and impressive trees including ficus, cola, and mahogany (Figure 3.1). Due to the economic importance of ecotourism, this part of the sanctuary is under the strictest local protection. Common forms of anthropogenic disturbance here include the maintenance of trails (e.g., trimming edges), discarded refuse, limited animal grazing and minimal disturbance of forest edges (e.g., small household dumps, limited animal grazing, personal trails).

Figure 3.1: Unlogged Western Forest. The tall primary trees in western “core” forest provided numerous arboreal pathways for both colobus and guenons and were themselves attractions on ecotourism tours. Owing to its great size, this particular ficus was a typical stop on most tours.
South and southwest of the village of Boabeng, small patches of the forest were cleared in the past and used as small farm plots. Though they are now protected as part of the sanctuary, the remnants of these patches remain in the form of regenerating farmland. The time when villagers ceased farming this part of the forest is unclear, but local farmers I spoke with typically placed the date around the late 1970s to early 1980s. In this part of the sanctuary, these former small farm plots were separated by thin corridors of primary forest and were characterized by a low understory dominated by short grasses and other types of herbaceous vegetation (Figure 3.2). A few tall trees were located within these regenerating pockets of farmland and were likely maintained in the past as shade trees. Along the southern edge of the village, large refuse dumps, permanent latrines, and pig sheds were located just along the forest edge. Due to the proximity of these locations to the forest, rains would frequently wash refuse out of trash heaps and deep into the forest. The disturbed edge forest adjacent to these locations was characterized by small trees (including species atypical of the primary forest), dense vine-tangled understory, and less enclosed canopy with fewer arboreal pathways between tree crowns.
Figure 3.2: Regenerating Farmland. This photo shows an area of regenerating farmland southwest of the village of Boabeng. Note the low vegetation forming the understory and the few large primary trees that were not felled – remnant shade trees from the past use of this area as farmland.

Study Groups

Large groups of both of the most common primate species at BFMS, *C. vellerosus* and *C. campbelli lowei*, ranged across unlogged western forest and more disturbed southern forest. Under most circumstances, these groups were well-habituated (see chapter 4 for a more complete description of the species habituation level). This allowed for close observation of positional behavior when these animals were accessible (i.e., not obscured by understory scrub).

To compare the positional behavior and habitat usage patterns for conspecifics of each species, I included four general study groups. For the colobus
(C. vellerosus), these groupings were straightforward. One group, named Wawa, utilized a range directly west of the village of Boabeng but included more disturbed forest at the southern extent of its range. The second group, named Redtail, ranged south and southwest of the village in more disturbed forest habitat. The names of these groups were created by previous researchers though they have come to be used frequently by locals as well. The ranges of each group overlapped along the southern extent of Wawa’s range and the western extent of Redtail’s range but neither group relied heavily on this part of the sanctuary (Wawa ~5% of observations; Redtail ~2% of observations). The total overlap between the ranges was not quantified but comprised a minimal proportion of their total home range. The observed ranges of each colobus group along with the approximate extent of overlap between the two group’s home ranges are presented in Figure 3.3.
Figure 3.3: Wawa and Redtail Colobus Home Ranges. This map depicts the observed range of colobus study groups included in this study. The Wawa colobus group ranged across the unlogged forest west of Boabeng while the Redtail colobus group ranged south and southwest of the village. The figure also shows the approximate area of overlap between the two colobus groups where their ranges met southwest of the village of Boabeng.
Choosing guenon (*C. campbelli lowei*) study groups was more challenging. Prior to this study, the ranges utilized by guenon groups at BFMS were incompletely known. I began the study following groups of guenons found in similar though not identical ranges as the two colobus groups. Two guenon groups, referred to locally as Guide’s Group and Methodist Group, ranged directly west of the village. Three factors made distinguishing between these groups difficult. First, the groups’ daily ranges overlapped greatly. Second, the groups frequently moved together across their habitats—likely as a means to defend their own access to village food resources. Third, the undergrowth, even in the less disturbed forest west of the village, was very dense. Consequently, guenons moving at low heights through these areas were very difficult to observe and it was frequently not possible to determine where one group ended and the other began.

Because I was interested in differential use of positional behaviors and supports in certain habitats rather than group differences per se, I combined observations from both groups referred to here at Central Guenons. For similar reasons, I lumped observations of two adjacent guenon groups from the more disturbed forest south of the village of Boabeng into a single study population referred to here as Periphery Guenons. There was no overlap between the collective ranges of the Central Guenons and the Periphery Guenons. Instead, a small mostly-male band (with one observed adult female) ranged in the forest area southwest of Boabeng between these two groups. Figure 3.4 shows the observed ranges for these groups.
Figure 3.4: Central and Periphery Guenon Home Ranges. This map depicts the observed ranges of guenon study groups included in this study. The Central Guenons included two overlapping groups ranging west of the village of Boabeng in unlogged, primary forest. The Periphery Guenons included two overlapping groups ranging across the regenerating and disturbed edge forest south of Boabeng.
**Quantifying Forest Differences**

The forest west of the village of Boabeng exhibited a dense, interconnected arboreal canopy that likely contained a greater number of arboreal pathways for monkeys to exploit as they moved across their range than did the more disturbed and heterogeneous southern forest. The understory was dense in both areas of the forest but for different reasons. West of the village of Boabeng, this stratum consisted of densely clumped, immature tree stands separated by occasional thick patches of vine tangles. South of the village, the understory included fewer tree stands and more ubiquitous vine coverage. While these stark differences were visually apparent, I collected data on each area using two methods: forest plot sampling and canopy cover estimation.

**Forest Plots**

With the help of a local herbalist and his apprentice (Moses Kwasi Ampofo and Samuel Owuwu Adosah), I established a series of forest plot samples along alternating sides of the existing trail system. Due to the density of the understory throughout the majority of the sanctuary, plots sampled in deeper forest would have required substantial clearing of the understory and would have been counter to the goals of current conservation efforts and this field project. Each plot measured 7.5m (toward the forest core) by 15m (along the trail edge). Each subsequent plot was placed on the opposite side (whenever possible) of the trail at a minimum of 20
meters from the last. The strategy for placing plots throughout the majority of the forest is illustrated in Figure 3.5.

![Figure 3.5: Alternating Forest Plots Along Existing Trails.](image)

**Figure 3.5: Alternating Forest Plots Along Existing Trails.** This figure illustrates the placement of forest plots along alternating sides of the existing trail system. To prevent oversampling from the same general forest patch, at no point were plots placed within 20 meters of a previously sampled plot. Note that at the trail intersection shown at the bottom of the figure, the two alternating plots along the horizontal trail were spaced in such a way that neither would come within 20 meters of plots along the vertical trail.

For the areas of regenerating farmland southwest of Boabeng, I used a slightly different plotting method. A single trail crossed the outer edge of this former farmland and was cut in such a way that it passed far (>7.5m) from most remnant primary trees. Following the plotting method used elsewhere in the forest would have yielded data indicating that these patches were more open than they actually were. The low, grassy understory allowed passage deep into areas of regenerating
farmland without clearing the groundcover. As a result, I employed a plotting method more conducive to the architectural distribution of regenerating farmland trees. Beginning on the eastern extent of these fields, I constructed a 7.5m by 15m plot with the shorter edge set against the existing trail. For the subsequent plot, I shifted 20 meters down the trail, moved 15 meters into the field and created another 7.5m by 15m plot while maintaining the minimum 20m distance from the original plot. Each subsequent plot followed this initial pattern as depicted in Figure 3.6. Since both colobus groups included in this study used this regenerating forest, the different sampling methods should not bias intraspecific comparisons.

Figure 3.6: Plot Sampling in Regenerating Farmland. This figure illustrates the method used in placing plots along trails in the regenerating forests southwest of the village of Boabeng at BFMS. Note that plots penetrated deep from the trail as opposed to being placed along trail edges. Because remnant trees were typically found far away from trail edges, this sampling method better captured the distribution of trees found in regenerating farmland.
Within each plot, I recorded the following:

- **Location:** Each plot was given a number associated with a trail name (e.g., Akonkodie 3) and the corner points were recorded using a handheld GPS device for later reference.

- **Total Number of Large Trees:** I recorded the total number of trees with a Diameter at Breast Height (DBH) greater than 10cm. DBH was measured by hand using a measuring tape.

- **Large Tree Size:** I recorded DBH in centimeters for any tree with a DBH>10cm. Following Ganzhorn (2003), heavily buttressed trees were measured above the buttress, if possible. When not possible, the contribution of the buttress to the trees DBH was estimated and subtracted from total DBH. On rare occasions when large trunks separated into distinct boughs close to the ground, I measured DBH for each bough and summed them.

- **Total Number of Small Tree Stands:** I recorded the total number of tree shoots <10cm. Lianas and other vine coverage were not included in this count.

- **Estimated Vine Coverage:** Each plot was assigned to one of five categories based on the percent of the ground surface within the plot covered in vine tangles. These categories were 0%, 25%, 50%, 75% or 100%.
Canopy Density Estimate

In addition to forest plots, I estimated vertical canopy density. This was done by looking upward through a 2 cm diameter pipe at 5 m intervals along the existing trail system (as per Ganzhorn, 2003). The goal was to sample a vertical cross section of the canopy that could be compared between group ranges as an estimate of canopy interconnectedness. At each 5 m point, I recorded whether the opening at the other end of the pipe fell into one of the following three categories:

- **Open**: No part of the canopy (leaves, branches etc.) was visible.
- **Closed**: No sky was visible.
- **Partial**: Both sky and canopy were visible.

In order to later associate each canopy density estimate with a particular group’s home range (see below), I recorded each point using a handheld GPS device.

Associating Forest Difference and Study Group Habitat

Both forest plots and canopy density estimates were conducted throughout the existing trail system. Forest plots were additionally taken along the village edge. Canopy density estimates were not conducted along the village edge. Since all plots sampled and canopy density estimate points were located along trail systems and plotted using GPS, I was able to compare them to the estimated range used by each study group during the observational period. Below, I offer qualitative descriptions of the forest habitats of each group and present quantitative results for forest plots and canopy density estimates for each group’s observed range.
**Forest Differences for Colobus**

**Western Forest: The Range of the Wawa Colobus Group**

Wawa Colobus ranged across some of the least disturbed forest area at BFMS. Permanent alterations of western forest included one of two primary dirt roads entering the village of Boabeng, clearings for tourist attractions such as the monkey cemetery and large ficus trees, wide trails, and an isolated shrine. Despite these disturbances, the canopy in this area was densely interconnected with many available arboreal paths across roads and trails. Near the village edge, the forest exhibited clearer signs of long-term disturbance (i.e., novel tree species, stunted forest trees, and open patches of disturbed understory). The southern extent of the Wawa Colobus’s range was the most disturbed with wide patches of regenerating farmland and more extensive disturbed edge forest along the village’s southwestern border.

**Southern Forest: The Range of the Redtail Colobus Group**

Redtail Colobus were located in the more disturbed forest south and southwest of the village of Boabeng. While the trail system was less extensive south of the village than in western forest, several of these trails were quite wide and capable of accommodating small tractors. Fallen or previously logged trees produced patches of disturbed forest characterized by extremely dense understory vegetation that, in turn, prevented the reemergence of a new canopy layer. More intact primary forest wrapped around what I called mixed disturbed forest. This
“mixed disturbed” forest exhibited numerous shorter trees, often of species different than those found deeper in the primary forest. A narrow corridor of primary trees allowed access to the village’s southern border. Southern forest understory consisted primarily of stunted or dead saplings strangled by tall heaps of vine-tangled vegetation. Southwest of the village, Redtail Colobus’s range overlapped that of Wawa Colobus in a portion of the regenerating farmland described earlier.

**Canopy Density and Forest Plots in Colobus Ranges**

Partial coverage comprised the largest proportion of canopy density estimates for both forest types (see Figure 3.7). However, the Wawa Colobus group's home range included a larger proportion of closed canopy estimates than did the home range of the Redtail Colobus group (Wawa Colobus group: 36.4% of all point estimates; Redtail Colobus group: 19.3% of all point estimates). Though one extra plot was sampled within the Wawa Colobus home range, these plots included 30 more large trees (trees greater than 10cm DBH) and a slightly larger number of trees per sampled plot than did the Redtail Colobus group’s more disturbed range (see Table 3.1). Differences in DBH between the two colobus group’s ranges were not significant (Mann Whitney U-test: p=0.571).
**Figure 3.7: Canopy Density Estimates in Colobus Home Ranges.** These graphs compare canopy density estimates for home ranges of the two colobus groups included in this study. For each observation, I looked through a pipe and classified the other end as Open, Partial or Closed (see text for definitions of each). In the less disturbed range of the western forest, I collected a total of 176 canopy density estimates for the Wawa colobus group. In the more disturbed range of southern forest, I collected 207 canopy density estimates for the Redtail colobus group.

**Table 3.1: Forest Plots in Colobus Home Ranges.** This table compares the results of forest plots sampled within two colobus home ranges. The data include: a) average diameter at breast height (DBH) for trees >10cm across each study groups’ home range, b) DBH for the largest trees within each groups’ home range, c) total number of trees >10cm (DBH) across each groups’ home range, d) average number of large trees (>10cm) per plot, e) minimum and maximum number of trees per plot within each groups’ range and f) total number of plots sampled per range. DBH was the only comparison between forests made using a statistical test and produced no significant differences (Mann-Whitney; p=0.571).
**Understory Density in Colobus Ranges**

Vine coverage estimates and tree stand tallies reveal substantial differences between the home ranges of the two colobus groups in the nature of their respective forest understories (see Figure 3.8, Table 3.2). The Wawa Colobus group’s less disturbed home range included, on average, fewer small tree stands per sampled plot than did the home range of the Redtail Colobus group (Wawa Colobus: 48.1 small trees per plot; Redtail Colobus: 34.4 small tree stands). Conversely, vine-tangled vegetation covered a larger percentage of plots sampled in the Redtail Colobus group’s home range compared to plots sampled in the Wawa Colobus group’s home range (Redtail colobus group: ~40% vs. Wawa colobus group ~10%).

**Figure 3.8: Vine Coverage in Colobus Home Ranges.** Each graph illustrates the percentage of forest plots sampled within each colobus group’s home range that fell into one of the five vine coverage estimates used in this study (see above for a description of this estimate).
<table>
<thead>
<tr>
<th>Study Group</th>
<th>a) Avg. Number of Small Tree Stands per Plot</th>
<th>b) Min/Max Number of Small Tree Stands</th>
<th>c) Total Number of Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>48.1</td>
<td>0/118</td>
<td>33</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>34.4</td>
<td>0/106</td>
<td>32</td>
</tr>
</tbody>
</table>

**Table 3.2: Small Tree Stand Density in Colobus Home Ranges.** This table compares tallies of small tree stands (<10cm) found within sampled plots for each of the colobus group’s home ranges. These data include: a) the average number of small tree stands (<10cm) across each groups observed range, b) the minimum and maximum number of small tree stands found within a single plot and c) the total number of plots sampled within a colobus group’s home range.

---

**Forest Differences for Guenons**

**Western Forest: The Range of the Central Guenons Group**

The Central Guenons utilized a range overlapping that used by Wawa Colobus but shifted slightly northward. Their range included less disturbed, unlogged areas of the western forest with numerous potential arboreal pathways open for travel between the range edges and across trails. The southern extent of their range lay on either side of one of the large dirt roads leading into Boabeng and did not continue into the regenerating forest patches further to the south. Canopy cover diminished towards the northern extent of their range, mostly resulting from fallen or dead trees rather than forest clearing. Members of the Central Guenon group spent much of their morning and evening hours along the disturbed edge of western forest bordering the village of Boabeng.
Southern Forest: The Range of the Periphery Guenons Group

Periphery Guenons utilized a range virtually identical to that of the Redtail Colobus with two notable exceptions. First, the two groups included within the Periphery Guenons moved farther south than did Redtail Colobus along a system of streambeds into mostly unlogged primary forest. Second, neither group of Periphery Guenons ever exploited the regenerating forest used by both the Redtail and Wawa Colobus groups to the southwest of the village.

Canopy Density in Guenon Ranges

Differences in canopy density between Central and Periphery Guenon groups were very similar to those found for the two colobus groups. The Central Guenons group’s home range exhibited a higher proportion of closed canopy than that of the Periphery Guenons (see Figure 3.9). Over 40% of the canopy density estimates in the Central Guenon group’s range was closed while less than 20% of canopy density estimates were closed in the Periphery Guenon group’s southern forest. Despite having two fewer total plots sampled in the Central Guenons range, there were 14 more large trees within their range (see Table 3.3). I found no significant difference in average DBH between the home ranges of Periphery and Central Guenons (Mann Whitney U-test: p=0.57).
Figure 3.9: Canopy Density Estimates in Guenon Home Ranges. These graphs compare the percent of open, partial and closed forest recorded during canopy density analysis for the Central and Periphery Guenon groups. I collected 189 total observations within the Central Guenon Group’s range and 216 total observations within the Periphery Guenon group’s range.

<table>
<thead>
<tr>
<th>Study Group</th>
<th>a) Avg. Large Tree DBH</th>
<th>b) Max DBH</th>
<th>c) Total Number of Large Trees</th>
<th>d) Avg. Number of Large Trees per Plot</th>
<th>e) Min/Max Large Trees per Plot</th>
<th>f) Total Number of Plots Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>128.1cm</td>
<td>650cm</td>
<td>92</td>
<td>3.5</td>
<td>0/7</td>
<td>26</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>127.9cm</td>
<td>494cm</td>
<td>78</td>
<td>2.8</td>
<td>0/9</td>
<td>28</td>
</tr>
</tbody>
</table>

Table 3.3: Forest Plots in Guenon Home Ranges. This table compares the results of plots for Central and Periphery Guenon groups at BFMS. These data include: a) the average diameter at breast height (DBH) for large trees (>10cm) across each study group’s entire range, b) the DBH for the largest trees within each group’s range, c) the total number of trees >10cm recorded within plots across each group’s entire home range, d) the average number of large trees per plot, e) the minimum and maximum number of trees in a single plot within each group’s home range and f) the total number of plots sampled per home range. DBH was the only comparison between forests made using a statistical test and produced no significant differences (Mann-Whitney; p=0.57).
Understory Density of Guenon Ranges

Differences in the nature of the understory were even more pronounced between the home ranges of the Central and Periphery Guenons than between the home ranges of the two colobus groups (Figure 3.10, Table 3.4). 50% the plots sampled within the Periphery Guenon group’s home range were covered nearly entirely with vine-tangled vegetation. In contrast, approximately 15% of the plots sampled in the Central Guenon group’s home range were covered entirely in vine-tangles. The Central Guenon group’s range, however exhibited more tree stands per plot on average than did the Periphery Guenon group’s range (Central Guenons: 51.4; Periphery Guenons: 40.5).

Figure 3.10: Vine Coverage in Guenon Home Ranges. Each graph illustrates the percentage of forest plots found within Central Guenon and Periphery Guenon group's home range falling into one of five vine coverage estimates (see above for the description of this estimate).
<table>
<thead>
<tr>
<th>Study Group</th>
<th>a) Avg. Number of Small Tree Stands per Plot</th>
<th>b) Min/Max Number of Small Tree Stands</th>
<th>c) Total Number of Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>51.4</td>
<td>9/91</td>
<td>26</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>40.5</td>
<td>7/106</td>
<td>28</td>
</tr>
</tbody>
</table>

**Table 3.4: Small Tree Stand Density in Guenon Home Ranges.** This table compares small tree tallies for plots sampled within the home ranges of Central and Periphery Guenons at BFMS. These data include a) the average number of small tree stands (<10cm) across each group’s home range, b) the minimum and maximum number of small tree stands found within a single plot and c) the total number of plots sampled within each group’s home range.
Figure 3.11: Comparison of Western and Southern Forest Understories. These photos show the nature of understory density differences between vine heap dominated southern forest (upper) and dense tree stands in western forest (lower) at BFMS. The upper photo was taken in the southern forest area shared by the Redtail Colobus and Periphery Guenon groups. The lower photo was taken in the forest shared by the Wawa Colobus and Central Guenons. These differences typify the differences in understory density for most of the plots sampled in both forests.
Conclusion

Results of canopy and understory density sampling establish structural differences in support density between unlogged, western forest and the more disturbed southern forest at BFMS. West of the village of Boabeng, the forest is dense and the upper canopy more interconnected. With the exception of disturbed patches near the central sanctuary, along the road and near the village as well as regenerating farmland at the southern extent of their range, Wawa Colobus in western forest had opportunities to move via the upper canopy across the majority of their range. Even when colobus frequented the understory, pathways allowing movement back into the upper canopy were almost always nearby. Since their range did extend into regenerating forest, Central Guenons had access to a nearly uninterrupted upper canopy. The interconnected upper canopy found in this part of the forest helps explain why local ecotourism has been focused so extensively on this area.

The patchwork southern forest at BFMS was structurally distinct from the western forest. Upper canopy arboreal pathways may have existed here but were likely far more limited. This might explain why both species in southern forest tended to repeatedly follow the same upper canopy arboreal pathways as they moved between the edges of their respective ranges. While their western neighbors might move both vertically and horizontally through almost the entirety of their range, guenons and colobus in the southern forests would often move low along the vine-choked understory or along the existing trail system. I test whether these
anecdotal observations match data I collected for the relative use of forest strata by colobus and guenons in subsequent chapters.

**Summary**

1. Two colobus groups were included in this study. The Wawa Colobus group ranged in unlogged, primary forest west of the village of Boabeng. The Redtail Colobus group ranged across a mosaic of regenerating, edge and primary forest south of the village of Boabeng.

2. Four guenon groups were included in this study. Two overlapping groups found in unlogged, primary forest west of the village of Boabeng were grouped together to compose a larger sampled population called Central Guenons. Two overlapping groups found in mosaic southern forest were grouped together to compose a larger sampled population called Periphery Guenons.

3. I sampled the structural continuity of each study area using forest plot sampling and canopy density estimates. Within forest plots, I tallied and measured DBH of large trees (>10cm DBH), tallied small trees (<10cm DBH) and estimated the extent of understory vine coverage. Along existing trails, I estimated canopy coverage by looking through a tube and recording whether canopy was enclosed, partially visible or not visible. Both forest plots and canopy density estimates were recorded by GPS and associated with observed home ranges for each of the primate study groups.
4. The western forest was characterized by a more enclosed upper canopy, more large trees, and a dense understory dominated by small tree stands.

5. The southern forest was characterized by a more open canopy, fewer large trees, and a dense understory dominated by masses of vine-tangled vegetation.

6. These contrasts in forest architecture may have driven the intraspecific differences in positional behavior discussed in Chapters 5–7.
Chapter 4: Methods of Sampling and Analysis

Overview and Objectives

Between January and November 2010, I collected observational data on positional behavior and habitat usage for two species of non-human primate: the ursine colobus (Colobus vellerosus) and the Lowe's monkey (Cercopithecus campbelli lowei). The intent of this field study was to sample the frequency of certain postures and locomotor behaviors for each species throughout the year in areas of forest characterized by differing forest architecture. This study had the following objectives:

- To add the positional behavior profiles for each of these species to a growing body of literature aimed at quantifying behavioral variation across the Primate Order.
- To compare positional behavior profiles between conspecific groups living in close proximity to one another in structurally distinct forest habitats and to test whether positional behavior varies significantly between these habitats.
- To test for intraspecific sex differences in positional behavior within the least disturbed groups for each species.
To meet these objectives, I collected data on sex, maintenance activity, positional behavior, forest type, forest strata, and the size and orientation of supports using a three-minute focal sampling method. General explanations of these variables are provided later in this chapter and detailed definitions of the categories for each are provided in their respective chapters (ch. 5-7).

Methodological Issues in the Observation and Sampling of Positional Behavior for Wild Primates

The accurate and replicable sampling of positional behavior has long been a concern for many studying primate positional behavior. For example, “Ripley’s Challenge” is a term that derives from a 1965 conference in which the accuracy of attempts to associate morphology and locomotor behavior in nonhuman primates was questioned (Dagosto and Gebo, 1998). On grounds that behavioral studies conducted on wild primates were rare, often incompatible, and failed to represent the entire range of primate locomotor variability, some researchers have questioned whether previous attempts to correlate morphology and behavior provide an accurate understanding of form-function associations in living primates (Dagosto and Gebo, 1998). This challenge has spawned a debate over sampling methods, greater standardization in the categorization of primate postural and locomotor, behaviors and an acknowledgment of the limitations in comparing different studies of primate positional behavior.
One criticism leveled at studies of positional behavior is that previous studies have relied on different sampling methods producing potentially different outcomes. Bout sampling is a continuous sampling technique that attempts to tally the frequency of different locomotor or postural activities while accounting for differences in total duration between those activities (Dagosto and Gebo, 1998). In contrast, time sampling is an instantaneous sampling method focused on recording the frequency of different locomotor or postural activities at fixed time intervals (Dagosto and Gebo, 1998). To test the comparability of these methods, Dagosto and Gebo (1998) used both techniques to record shots witnessed during a series of 10 Chicago Bulls NBA games. They matched the results to official shot tallies for the games and found that bout sampling more accurately reflected the total shots per individual. However, an earlier study by Doran (1992) compared both these sampling techniques while observing the locomotor behavior and substrate use of the common chimpanzee (*Pan troglodytes*). She argued that bout sampling may over-represent the frequency of locomotor behaviors that occur frequently but for short durations. When duration is controlled for bout sampling, Doran (1992) found that the two methods produced effectively the same results.

Standardization of sampling methods, however, does not guarantee that studies of primate positional behavior will be comparable. The nature of primate behavioral observation forces primate researchers to parse fluid, continuous behaviors into discrete categories that can then be compared quantitatively (Hunt et al., 1996). Of course, such demarcation exposes research designs to the possibility of
introducing subtle variations between how individual researchers interpret certain behaviors (Dagosto and Gebo, 1998). The lack of clear distinctions between locomotor or postural categories and/or clear definitions of those categories published in the literature poses a serious challenge when trying to compare studies from different authors. Hunt et al. (1996) addressed this problem specifically by publishing a standardized set of well-defined postural and locomotor categories.

Another methodological concern in sampling primate positional behavior involves the randomization of sample subjects (i.e., the shift between individual focal primates during the course of an observational period). Time autocorrelation refers to the tendency for repeated sampling of an individual to over-represent certain behaviors, particularly those lasting for a long duration (McGraw, 1996a; Dagosto and Gebo, 1998). For example, by repeatedly sampling a single individual in the sit posture, an observer may artificially increase the likelihood that that each subsequent observation will also be sit because sit is a posture that often lasts for a long period of time. In order to avoid time autocorrelation, Dagosto and Gebo (1998) argued for a research design that focuses on independent (i.e., non-lumped) data for each individual animal under study. This method might avoid much of the bias that any differences in the frequency of samples for each individual may produce. Because such a technique requires the ability to recognize individual animals it is likely not suited for all primate field studies. McGraw (1996b) tested the biasing affects of time autocorrelation on his own large database of positional behavior samples for five cercopithecoid species in the Tai forest, Cote d’Ivoire and
found that spacing intervals between repeated samples of a single individual by at least 12 minutes minimized the dependency between samples. Maintaining this duration between samples forces the researcher to keep track of the spatial relationships of a number of recently sampled animals, but this sampling method may be useful under field conditions where individual animal identities are not known, cannot be reliably identified due to poor visibility, and/or cannot be ascertained given a short interval between time samples.

**Focal Sampling Methods Used in this Study**

**Duration:**

I began observational research at Boabeng-Fiema Monkey Sanctuary (BFMS) in the Brong Ahafo region of Ghana, West Africa at the end of January 2009. The two weeks prior to the study were spent acquiring necessary permits, following cultural protocols involving formal introductions to local community elders, chiefs and fetish priests, using GPS to map the forest trail system, and selecting habituated troops that met the objectives set forth in this project. Observational research continued throughout the year and ended due to personal injury in early the November 2010.

I included behavioral samples throughout as much of the year as possible in order to minimize potential seasonal bias in my dataset. The availability of plant-derived food items (e.g., leaves, fruits, seeds) contributing to non-human primate diets varies throughout the year for a number of reasons related to each individual plant species’ phenological patterns (e.g., periods of fruit/leaf production, presence
of secondary compounds or other anti-feedents) (Garber, 1987). In order to deal with seasonal variation in potential food resources, primates adapt their behavioral patterns in a number of ways. Adaptations to food scarcity or changing food availability might include: 1) overconsuming during periods of peak availability and relying on fat stores during lean periods, 2) reducing activity patterns and thus energy expenditure when food resources are unavailable, or, more commonly, 3) focusing on alternate food resources as more desirable resources disappear (Hladik CM, 1988). Because the distribution of food is known to influence postural tendencies (McGraw, 1998b), seasonal variation in food supply may affect long-term positional behavior patterns. Seasonal differences in positional behavior have been noted in at least one field study. Dagosto and Gebo (1998) found that the red colobus in the Kibale forest of Uganda increased the frequency of quadrupedal locomotion and decreased leaping and climbing during the dry season.

Since seasonal variation in diet has been reported from other sites for black-and-white colobus groups (Dasilva, 1994) and for numerous guenon groups (Gautier-Hion, 1980), seasonal dietary variation might be expected at BFMS as well. From conversations with local farmers, I learned that BFMS typically experiences a long dry season from November to February or March with a shorter dry period between July and August. The heaviest rains are expected in June and September but frequent rainfall is also expected between March and July (Saj et al., 2005). Changes in expected rainfall patterns can produce wide variation in the availability of human food sources. Throughout this study, farmers frequently complained about a
particularly poor rainy season, though I did not collect rainfall data to confirm this. Ongoing longitudinal studies of forest phenological patterns conducted by graduate researchers from the University of Calgary with the assistance of local conservation agents are documenting changing resource patterns at BFMS. In order to capture the effect that this change might have on *C. vellerosus* and *C. campbelli lowei* positional behavior and habitat usage, I collected behavioral samples in both the established dry and wet seasons. While an injury unexpectedly shortened this study, I employed a sampling method intended to ensure that behavioral samples for both species were comparable between forest types throughout the field project.

**Sampling Method:**

I used a three-minute instantaneous focal sampling method to record behavioral data for both primate species. Many recent studies of primate positional behavior have used time sampling methods (e.g., Doran, 1993; Garber and Pruetz, 1995; McGraw, 1996b,b; Youlatos, 2002; Bezanson, 2005) though the interval between time points chosen by individual researchers often varies. Some have argued that alternate sampling techniques (i.e., bout sampling) better reflect positional behavior (e.g., Dagosto and Gebo 1998). However, in order to compare results from this study with those of previous studies on closely related species (McGraw 1998a,b), instantaneous focal sampling was the most appropriate sampling technique for this study.
To monitor time between samples, I used a stopwatch with a repeating alarm set at three-minute intervals. Once the day's focal group was located, I started the watch. At each time point (i.e., alarm), I recorded the following data for the chosen focal animal:

- Observation time
- Focal animal's sex
- Maintenance activity: General activity in which the animal is engaged
- Positional behavior category: Focal animal’s current postural or locomotor category
- Support characteristics: The height, orientation and size of the focal animal's current support

Following each focal sample, I switched to that subject's nearest adult neighbor provided that that individual had not been sampled within the last 12 minutes. Subsequently, I followed the new focal subject until the next time point. Focal opportunities were skipped if one of the following four conditions was met:

1. No adult animals were visible
2. Only adults that had been previously sampled within the last 12 minutes were visible
3. The current focal animal moved out of visibility
4. The focal animal was agitated by tourists or locals (see Habituation below)
Maintenance Activity:

Studies of positional behavior offer an opportunity to not only identify and model associations between primate anatomy and behavior but also to create testable hypotheses grounded in socioecology regarding why certain postural or locomotor patterns are found in a particular species. For example, the frequencies of different locomotor behaviors (i.e., leaping vs. climbing) are undoubtedly influenced by the morphology of a primate’s musculoskeletal anatomy. However, knowing whether these behaviors occur more often during aggressive social activity, short-distance foraging movement, or long-distance travel may provide information about a primate’s reproductive strategies, feeding ecology, and range use. McGraw (1996b) demonstrated that when comparing species with significant differences in positional behavior it is important to consider how general behavioral characteristics are associated with postural or locomotor activities. These behaviors, called “maintenance activities,” help to contextualize observed patterns of positional behavior in terms of their relationship to the ecological or social realities of a primate’s environment.

In this study, I compare overall positional behavior patterns between focal groups and examine positional behavior in the context of particular maintenance activities. Maintenance activities associated with postural categories (i.e., body mass largely at rest) included the following: active feed, food processing/acquisition, rest feed, rest, and rest social. Maintenance activities associated with locomotor categories (i.e., majority of body mass in motion) included the following: non-social
locomotion and social locomotion. Maintenance activities associated with posture
are defined in Chapter 6 and maintenance activities associated with locomotion are
defined in Chapter 7.

Positional Behavior:

Positional behaviors, like all behavior, are not static, discrete phenomena but
rather are part of a sequence of continuous postures or movements grading into one
another. To be amenable to observation, testing, and comparison, I attempted to
categorize these continuous behaviors and treat them as though they were isolated
actions. Of course, this presents a number of practical problems already discussed
from standardization of terms to the degree of precision both reliable under field
conditions and meaningful for interpretation. While the list of standardized terms
provided by Hunt et al. (1996) helped to establish definitions of behaviors, I judged
the list of 32 broad postural/locomotor categories and dozens more subcategories
to be too cumbersome to use in field conditions. Locomotor/postural descriptions
were frequently too detailed for practical use, especially since visibility was often
compromised and focal animals not seen in their entirety. Additionally, while these
descriptions might provide important information for understanding primate
biomechanics, it is not clear what significance minute differences in postures would
have for understanding broad socioecological strategies. Instead, I follow McGraw
(1996b) and others in grouping variables into larger, broader positional behavior
categories to better associate gross differences in positional behavior with
differences in their forest architecture. Positional behaviors used for analysis in this study are listed and defined in Table 4.1 and illustrated in Appendix A.

<table>
<thead>
<tr>
<th>Pooled Postural Categories</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cling</td>
<td>Supporting body mass on the side surface of a support usually by grasping with hands and/or feet</td>
</tr>
<tr>
<td>Recline</td>
<td>Supporting body mass on primate’s side or stomach</td>
</tr>
<tr>
<td>Sit</td>
<td>Supporting body mass on primate’s ischia or thighs</td>
</tr>
<tr>
<td>Stand</td>
<td>Supporting body mass on two, three or four limbs</td>
</tr>
<tr>
<td>Other</td>
<td>All postures not included in the previous categories</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pooled Locomotor Categories</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drop</td>
<td>Descent between supports with negligible propulsion</td>
</tr>
<tr>
<td>Horizontal Climb</td>
<td>Movement between supports propelled by grasping and pulling oneself to a proximate support and/or pushing off of an initial support</td>
</tr>
<tr>
<td>Leap</td>
<td>Propelled movement between discontiguous supports. Must include an aerial phase.</td>
</tr>
<tr>
<td>Vertical Climb</td>
<td>Propelled vertical descent or ascent along one or more supports</td>
</tr>
<tr>
<td>Quadrupedalism</td>
<td>Travel along a single support propelled on three or four limbs</td>
</tr>
<tr>
<td>Other</td>
<td>All locomotion not included in the previous categories</td>
</tr>
</tbody>
</table>

Table 4.1: Locomotor and Postural Behaviors Defined.

Support Characteristics

In order to quantify habitat usage, at each three-minute time point, I recorded data on support height, size and orientation. Support height was a measure of how high the animal was from the ground at a given focal point and was estimated in 5m intervals. Support size was a categorical estimate of both the size and support capabilities of a chosen substrate. Support orientation was an estimate of the degree to which a chosen support was angled in comparison to a horizontal ground plane. The categories recorded for support characteristics followed those
used in previous studies (e.g., Fleagle, 1976; McGraw, 1996b; Garber and Pruetz, 1995) and each category is described in detail in Chapter 5.

**Daily/Annual Follow Routine:**

**Daily Follows:** In the unlogged western forest at BFMS, I began searching for *C. campbelli lowei* shortly after dawn (~6:00am) and followed them continuously until they began raiding the village in the mid-afternoon (between 1:30pm-4:00pm). Village raids consisted of movement between houses, across roofs, and within courtyards. Such raids typically lasted until late in the evening and targeted the villagers’ preparation of the evening meal. Due to the difficulty of following the animals through the village, the increase in human-monkey interaction during village raids, and the lack of applicability of this behavior to answering my research questions, I chose not to follow the animals during this time.

In the disturbed forest south of the village, the focal schedule for *C. campbelli lowei* was slightly altered. I began searching for the monkeys shortly after dawn and followed the animals until they either raided the village (as in the undisturbed forest but usually occurring around 3:00pm) or until they moved south and out of the visible range of the existing trail system.

In both western and southern forests, *C. campbelli lowei* groups consistently slept out of view from existing trails and moved towards the village along one of several regular pathways. This facilitated locating the groups each morning once they began moving but made them difficult to find before this initial move. As a
result, I initiated most follows once the groups began their slow foraging travel towards the village edge.

For both groups of *C. vellerosus*, I began follows shortly after dawn (~6:00 am). I followed each group continuously throughout the day with a few exceptions. Colobus in both western and southern forest would sometimes descend to the forest floor and move within a particularly dense area of forest between the southwest edge of the village and nearby trails. Depending on whether colobus opted to rest within this edge forest or simply travel through it, they were sometimes not visible for long periods of the day. Additionally, colobus also raided the village at least once a week. For the duration of these raids, I did not record behavioral data.

Typically, each colobus group would have a long resting period throughout the late afternoon followed by a short feeding bout and then travel to a new locale. I terminated daily follows after this first late afternoon move that usually occurred between 4:00pm and 4:30pm. Very often, this late afternoon move brought colobus high into the upper canopy in or near their sleeping tree. Following colobus to this point in their daily routine facilitated finding them the following morning. On several occasions, *C. vellerosus* did move to a distant part of their range later in the evening after I had ceased the daily follow. Even in these circumstances, the home ranges and favored sleeping locations of both groups were well known and individuals were usually found early the following morning.

**Species Rotation:** To ensure a representative sample of observations for each species/study group (see chapter 3) throughout the year, I employed a rotating
schedule between species that included five-day follows for each study group. In other words, I normally followed each of the study groups for five consecutive days, switching to the next group on the following list beginning on the subsequent week: 1) *C. vellerosus* in unlogged forest, 2) *C. campbelli lowei* in disturbed forest, 3) *C. vellerosus* in disturbed forest and 4) *C. campbelli lowei* in undisturbed forest. These follow periods were usually conducted over consecutive days (i.e., barring illness, injury, or necessary trips away from the field site). Particularly in regards to the colobus groups that I followed until early evening, observations over consecutive days minimized the amount of time spent in the morning finding the group’s sleeping location from the previous evening.

**Habituation:**

All primate groups were habituated to human observation. Both species are the primary focus of ecotourism at BFMS and are frequently observed by both tourists and local villagers. Additionally, long-term researchers and students from an annual field school have been studying these groups the past decade. For example, *C. vellerosus* at BFMS have been under observation continuously by researchers since 2000. Though wary of nearby humans, *C. vellerosus* frequently fed along the edge of heavily traveled trails. Young adult males and mothers with infants were most likely to react to observing researchers or passing villagers but other group members tolerated human observers within a few meters.

*C. campbelli lowei* has not been the focus of recent published research at BFMS. However, for several years, student researchers participating in an annual
field school run by the University of Calgary have included various guenon groups found adjacent to the village in unlogged western core forest (Central Guenons among others) in their short-term observational projects. Additionally, Central Guenons often approached visiting tourists with the hopes of being fed. The Periphery Guenons found south of the village of Boabeng were less habituated than the Central Guenons in the western core forest. These groups were not regularly fed by visiting tourists and rarely approached humans as they walked along trails in this part of the forest. Nevertheless, the Periphery Guenons frequently raided the village and witnessed humans (both locals and visitors) traveling down trails within their range. As a result of this frequent interaction, the Periphery Guenons reacted to human observation (i.e., threat vocalizations, fleeing) only when humans directed actions toward them (i.e., children throwing dirt, tourists shouting at them) or came within extremely close proximity (i.e., a few meters).

Despite the high degree of habituation at BFMS, *C. vellerosus* and *C. campbelli lowei* groups exhibited strong reactions to observers under two conditions: the presence of large or loud tourist groups and human movement off of the trail system. Tourist groups, especially large school groups, frequently moved noisily through the forest (e.g., singing, blowing into horns, talking loudly, shouting at animals). Groups of *C. vellerosus* in both western and southern forests responded to noisy visitors either by moving high into the canopy or, if access points to the upper canopy (e.g., trunks capable of being climbed) were unavailable, by moving away from trails. *C. campbelli lowei* groups exhibited different reactions depending on
their past experience with humans. *C. campbelli lowei* in western forest often directed movement towards tourist groups of all sizes in the hopes of getting fed. During tourist feeding, most group members of *C. campbelli lowei* approached to within arms-reach of any tourist offering food. Periphery Guenon groups were more timid about close observation by visiting humans. I never observed these southern forest guenons approach human visitors for food. For both species in all parts of the forest, humans (i.e., villager, tourist or researcher) moving off the existing trail system elicited strong reactions (e.g., threat grunts, moving deeper into dense understory, moving high and out of human reach in the canopy).

Dealing with these habituation issues was challenging. It was apparent early in the study that I would have to compromise observational time to fit within the mission of the ecotourism industry promoted by my hosts in the BFMS Management Committee. Tourist groups regularly visited the site (typically several a day) though there was a great deal of variation in the number of groups that came as well as their arrival time. Whenever a large or noisy tourist group approached to observe my weekly focal animals (a period that could last from a few minutes to a half an hour), I would stop recording focal observations until the visitors moved. The Central Guenons in the western forest would often move with the tourists to maximize the amount of food they could gather. If this occurred while I was taking data, I would try to locate the adjacent Central Guenon study group.

Early in the study, I attempted to follow animals as they moved deep into the understory between forest trails. These were areas with very poor visibility and
dense vegetation that impeded my ability to follow. Both monkey species reacted strongly to these attempted follows off the trail, resulting in researcher-induced locomotor behaviors (i.e., fleeing) and threat vocalizations. In order to minimize my influence over the positional behavior of my research subjects, I discontinued follows whenever either species moved into an area far from view of existing trails. Usually, these pauses in observation time were minimal (i.e., a few missed time points) but could be extensive (i.e., several hours) if the animals moved into an area of poor visibility for extended periods of rest or feeding. Because C. campbelli lowei were smaller, often concealed within dense vegetation searching for insect prey and generally found lower in the canopy, I switched to the adjacent focal group within the same forest type when one group disappeared for an extended period of time.

Data Analysis

Focal data recorded on field notes were transcribed into a digital database and then analyzed using the SPSS statistical package. I used two similar methods to test for statistical differences: the G-test and the Fisher Exact Test. Both tests can be used to identify the likelihood that row and column variables in contingency (i.e., frequency) tables are independent and are sometimes referred to as Row x Column (R x C) tests of independence (Sokal and Rohlf, 1995; McKillup, 2005). R x C tests have been used to compare populations in previous studies of primate positional behavior (e.g., McGraw, 1996).
The two $R \times C$ tests used in this study differ in the manner in which they identify statistically significant dependent relationships between row and column. G-tests estimate the chi-square statistic to predict the probability that two frequency tables are independent and are sometimes referred to as log-likelihood ratios (McKillup, 2005). G-tests are subject to Type I error (i.e., detecting significant differences when there are none) when small sample sizes are used (Sokal and Rohlf, 1995). McKillup (2005) noted that within frequency tables with more than 20% of the expected cell frequencies less than 5, the G-test may be biased and should not be used. In contrast, the Fisher Exact Test finds the actual probability of generating frequency tables more extreme (i.e., more significantly different) than the table that is being tested, is not biased by small sample size and generates results very similar to the G-test (Sokal and Rohlf, 1995). The Fisher Exact Test is, however, computationally more difficult than the G-test, and even with computers, comparisons become untenable with large numbers of categories and/or large frequencies in each category. Fortunately, the large sample sizes that make the Fisher Exact Test more difficult to compute frequently will exceed the threshold needed to for reliable G-tests (Sokal and Rohlf, 1995). The similarity between the results of each method allows researchers to depend on both methods when comparing frequency data.

In this study, I rely primarily on the Fisher Exact Test whenever computationally possible (i.e., the computer could calculate test statistics in a reasonable time period). G-tests were used when the Fisher Exact Test could not be
computed efficiently. When sample sizes were particularly small or when Fisher Exact Tests could not be used but the minimum requirements for using the G-test were not met (i.e., no more than 20% of categories in a frequency table could have an n<5), I did not run a statistical comparisons between frequency tables. A significance value of 0.05 was used for both G-tests and Fisher Exact Tests. Probability results below the significance value for any contingency table indicated that the row and column variables exhibited a statistically dependent relationship of some sort. Though these tests do not illustrate what differences drive the dependent result or what the nature of that dependency might be, significant results for these tests have been used in past positional behavior studies to indicate significant differences between either column or row categories (McGraw, 1996b). For example, significant results of either the G-test or the Fisher Exact Test (p<0.05) when comparing colobus groups (row variable) in the overall frequency of certain locomotor behaviors (column variable) would indicate that each group differed to a greater degree than predicted by random chance in their overall locomotor profiles (Table 4.2).
Table 4.2: Illustration of R x C Statistical Tests. This frequency table compares all focal samples for female colobus during non-social locomotion. Row variables are the two colobus groups while column variables include six locomotor behaviors. At a 0.05 significance level, the results of R x C tests indicate that the groups and locomotor behavior show no significantly dependent relationship. In other words, both groups exhibit statistically equivalent locomotor profiles.

Summary

In this chapter, I described the sampling protocol, methodological challenges and analytical methods structuring this project. The following summarizes the most significant methodological elements of this study:

1. I used an instantaneous focal sampling protocol to record data on the support usage and positional behavior of guenon and colobus groups ranging in areas of forest characterized by differing levels of anthropogenic disturbance and forest architecture.

2. Each study group (n=4) was followed on rotating, five consecutive-day periods from January to November 2009. I followed colobus groups from just after dawn until their late afternoon move high into the forest canopy. I followed guenon groups from just after dawn until their evening village raids.
3. Habituation levels for both monkey species typically allowed for close observation from existing trails but the presence of tourists, the nature of the understory, and the monkey's wariness of off-trail movement placed limitation on my ability to conduct uninterrupted observations.

4. I transferred data collected through these observations into frequency tables that I compared using one of two Row x Column statistical methods (the Fisher Exact Test and the G-test).

5. These analytical methods test for dependent relationships between variables used to generate frequency tables. In this study, these methods were primarily used to test for statistically significant intraspecific differences between groups in their support preference and use of postures or locomotor behaviors.

Using the results of the sampling protocol and analytical methods described in this chapter, I compare profiles for support/forest strata usage (chapter 5), postural behaviors (chapter 5) and locomotor behaviors (chapter 6) between study groups for females of each monkey species. Due to the potential for sex differences to influence observed positional behavior, statistical comparisons are made only on females in Chapters 5–7. In chapter 8, I use the same methods to identify any intraspecific differences between males and females for both species in the least disturbed habitat at BFMS.
These results provide positional behavior profiles for both *C. vellerosus* and *C. campbelli lowei* and test whether the differences in forest architecture described in the previous chapter are sufficient to produce significant alterations in the positional behavior profiles of these two species in disturbed southern forest.
Chapter 5: Forest Strata and Support Usage

Introduction

In Chapter 3, I described the qualitative and quantitative differences in forest architecture between two pairs of home ranges at BFMS. A largely disconnected upper canopy and an understory dominated by dense, heaping masses of tangled vegetation characterized the portion of southern forest utilized by my study groups. In contrast, the western forest, though disturbed in portions, exhibited a more intact upper canopy and an understory that was dense due to closely packed tree saplings rather than tangled vegetation. In this chapter, I test whether the primate groups in these structurally distinct habitats utilized supports differently within their respective ranges.

For highly arboreal primates, Boughs, Branches, Trunks, Vines and Twigs provide the context for most observable positional behavior. The true distribution of these types of supports is difficult to quantify in a dynamic forest environment (e.g., the frequency of all Boughs compared to Branches across a primate’s entire home range). However, given the architectural contrasts between more disturbed southern forest and less disturbed western forest, we might expect the distribution of supports to differ between these two study areas. If support size and orientation influence a primate’s locomotor and postural behavior (Napier, 1967; Fleagle, 1980;
Demes et al., 1995; Schmitt, 2003), differences in likelihood of encountering supports of different sizes and orientations could significantly impact the positional behavior tendencies of animals moving within these forests. For example, a primate moving in a forest characterized by a more patchy distribution of its preferred supports would likely face different locomotor challenges than an animal moving in a more homogeneous environment.

Differences in forest structure and differences in support usage are related phenomena, but one cannot always infer the latter from the former. That is, primates inhabiting forests that differ structurally with respect to forest architecture need not necessarily use different support types. For example, McGraw (1996a) found that for four of five cercopithecoid species studied, there was no significant difference in support use by the same species in forest habitats characterized by differing levels of disturbance. The author attributed this consistency to the “active selection of a subset of supports” (p. 520) displayed by both larger- and smaller-bodied primates. In effect, these monkeys were choosing to use supports sharing similar characteristics even when those supports were not equally available.

If monkeys at BFMS were exhibiting a consistent preference for the same types of supports, variation in positional behavior might not necessarily be expected. On the other hand, if groups living in more disturbed southern forest were using supports with different characteristics than conspecifics in less disturbed western forest, these differences in support usage might offer one possible
explanation for any significant differences in either posture (Ch. 6) or locomotion (Ch. 7) between these groups. Here, I test for intraspecific differences in support usage and forest strata preference for *Colobus vellerosus* and *Cercopithecus campbelli lowei*.

**Hypotheses**

- **Research Question:** Do *C. vellerosus* and *C. campbelli lowei* living in structurally distinct forest habitats utilize supports of differing sizes, heights and/or orientations?

I made the following predictions regarding intraspecific variation in the use of support heights, sizes and orientations summarized in Table 5.1.

<table>
<thead>
<tr>
<th>Predictions</th>
<th>Intraspecific Support Use Differences</th>
<th>Possible Cause</th>
<th>Type of Change in More Disturbed Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₀</td>
<td>No change for either species</td>
<td>Morphological constraints</td>
<td>No change; statistically similar pattern of support usage</td>
</tr>
<tr>
<td>H₁</td>
<td>Both species change</td>
<td>Less interconnected canopy</td>
<td>Increased use of branches and twigs, lower supports and non-horizontal supports</td>
</tr>
</tbody>
</table>
| H₂          | Change in guenons but not colobus    | Combined effects of body size and the location of preferred food items | - Colobus: No change  
- Guenons: Increased use of low-lying, thinner supports and/or vertical supports |

Table 5.1: Predictions for Intraspecific Differences in Habitat Usage.
H0 predicts that species will exhibit no significant intraspecific difference in habitat usage profiles between study groups. Consistency in support use between members of the same species inhabiting architecturally distinct forests could be maintained by selecting supports sharing a set of common characteristics (i.e., similar sizes and orientations) irrespective of the availability of those supports (McGraw, 1996a). Further, colobus and guenons might also selectivity travel in particular forest strata, perhaps due to the location of preferred food items (McGraw, 1998b). In other words, to meet their species-specific goals (e.g., acquiring desired food items, resting comfortably, maintaining vigilance) each species is predicted to exhibit clear support and height preferences that do not change between forest types and are not influenced by differences in forest architecture.

H1 predicts that both species will choose to alter their patterns of support use in ways that facilitate travel across their respective ranges. Some researchers have suggested that primates should strive to shorten arboreal pathways whenever possible in order to better compete with other group members and to defend territory (Cant and Temerin, 1984). When canopy gaps prove too risky or costly to cross, primates might choose alternate pathways (Cannon and Leighton, 1994). Rather than being constrained by supports of a particular type (e.g., those capable of supporting their weight), both species at BFMS might increase their use of less preferred forest strata if those strata better facilitate daily activities (e.g., foraging, range defense). In order to travel across the center of their respective ranges in more disturbed southern forest where primary trees were more sparsely
distributed, Periphery Guenons and Redtail Colobus might include more frequent use of thinner supports that dominated the layer of tangled vegetation dominating southern forest understory. Vertical (i.e., trunks) and oblique supports are common across the forest understory and I predict that they will be used at higher frequency in southern forest.

H$_2$ predicts that $C.\ vellerosus$ will be less likely to alter its support use profile in more disturbed habitat than do $C.\ campbelli\ lowei$ for two reasons. First, body size may limit the larger-bodied $C.\ vellerosus$ to fewer support options than it did for smaller-bodied $C.\ campbelli\ lowei$. Larger-bodied primates must find supports capable of bearing their weight (Fleagle, 1985). Body weights of the study subjects were not collected during this project; however, body masses published by Delson et al. (2000) are listed in Table 5.2. $C.\ vellerosus$ females, being on average nearly three times as heavy as guenon females, might be assumed to have a more limited range of supports available to them. Unable to use alternate supports, this could limit possible support options more for $C.\ vellerosus$ than for $C.\ campbelli\ lowei$ females and may produce a more consistent support usage profile between colobus groups than between guenon groups.

<table>
<thead>
<tr>
<th>Female Body Mass</th>
<th>Lowest</th>
<th>Highest</th>
<th>Avg. Body Mass</th>
<th>Total Female Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C.\ vellerosus$</td>
<td>6200g (13.66lbs)</td>
<td>7500g (16.53lbs)</td>
<td>6860g (15.12lbs)</td>
<td>5</td>
</tr>
<tr>
<td>$C.\ campbelli\ lowei$</td>
<td>1800g (3.97lbs)</td>
<td>5000g (11.36lbs)</td>
<td>2563g (5.65lbs)</td>
<td>14</td>
</tr>
</tbody>
</table>

**Table 5.2: Body Mass for Female $C.\ campbelli\ lowei$ and $C.\ vellerosus$.** Body masses were collected from various institutions and published by Delson et al. (2000).
In addition to differences in support availability, $H_2$ predicts that differences in the diets of *C. vellerosus* and *C. campbelli lowei* will also influence the degree of intraspecific difference in support usage profiles, if any, between forest types. Oates (2005) noted that "banqueters," primates such as folivorous colobus, feed on large patches of abundant food resources (i.e., leaves), face less competition, move together between food sources (i.e., feeding trees), and can typically park themselves in a single location during a single feeding bout. Even in disturbed forest at BFMS, leaf resources might be ubiquitous enough that colobus there do not need to alter their use of supports or travel to different levels of the canopy to meet their daily dietary needs. In contrast, if *C. campbelli lowei* exhibit a diet very similar to that of the closely related *C. campbelli campbelli* (high fruit consumption supplemented by insects: Buzzard, 2006), the sparser, southern forest upper canopy might not offer the nutrient base capable of supporting the numerous guenon groups found there. In attempting to acquire alternate food resources (e.g., discarded human foods, insect larva found in the dense vine-tangled understory, low-lying fruit trees) guenons in the southern forest might frequent lower strata and more often use the thin, flexible supports found there (e.g., lianas, tree saplings, and flexible low-hanging branches). In $H_3$, colobus are predicted to be able to find upper canopy food resources more easily and to conserve their habitat usage profiles. Conversely, guenons that feed on resources that are more patchily distributed, such as fruits and non-social insects, are predicted to alter their support
usage profiles to meet their more competitive dietary demands (Garber, 1997; Oates, 1987).

**Methods**

To assess each group's support usage, I used a three-minute instantaneous focal sampling method. The sampling methods, statistical comparisons and study groups are described in detail in Chapter 4. On each time point, I recorded the size and orientations of supports used by a focal animal and the forest stratum in which those supports were located. To avoid the potentially confounding affects of sex differences, only females from the four groups were included in this analysis. I compare male and female patterns of support use in Chapter 8.

There were several challenges in accurately identifying the particular substrate used by a focal animal. During both postural and locomotor behaviors, primates frequently balanced their weight over multiple supports at one time. For example, when colobus sit, they often fully extend their lower limbs, sometimes draping them over an additional support (Morbeck, 1977). When these supports were of different size or orientation categories, the support judged to bear the majority of the focal subject’s weight was recorded (Figure 5.1).
An additional challenge arose in classifying the supports used in leaping behaviors that by definition include a period during which no limbs are in contact with a support (Hunt et al., 1996). When animals leapt, I recorded characteristics for the takeoff support but not the support where the animal landed. While both the initial support and terminal support are of significance to the biomechanics of primate leaping (Demes et al., 1995), I only recorded the initial support for two reasons. First, I needed to establish a standard for all observations that would enhance the comparability of these data following the field study. Standardizing observations prevented me from sampling takeoff supports during some leaps and
landing supports on others, obscuring any potentially significant differences between the two. Second, individuals of both species would often carefully select a support from which to leap, sometimes moving between several available options, suggesting that initial supports were a particularly important component to their leaping decisions.

Forest strata and support size and orientation categories are defined in separate sections below.

**Forest Strata**

The height of supports used by focal animals was estimated in 5m intervals from a horizontal plane on the ground. Each height was estimated visually and rounded to the nearest 5m increment. One exceptional case was when monkeys used arboreal supports located 2m or less above the forest floor. In these instances, the actual height of the support was recorded as <5m to distinguish them from purely terrestrial supports.

For analysis, I grouped height estimates that shared similar architectural features. I recognized the following four strata (illustrated in Figure 5.2):

- **Stratum I: Ground** – This layer included any terrestrial support (i.e., animal is supported primarily by the ground).

- **Stratum II: ≤5 meters** – This layer included the forest understory (e.g., young trees, vine-tangled vegetation, low-hanging branches).
• **Stratum III**: 10–15 meters – This layer included a portion of the crown of medium-sized trees and low-hanging supports of the upper canopy.

• **Stratum IV**: 20+ meters – This layer included the majority of the upper canopy. Heights in excess of the 20 meters were too great to estimate with any accuracy so all observations in which monkeys traveled to greater heights were grouped together within this category.

![Forest Strata Diagram]

**Figure 5.2: Four Distinct Forest Strata at BFMS.**

**Support Type**

Fleagle and Mittermeier (1980) divided supports into three categories based on their relative diameters: Bough (>10cm), Branch (≥2cm≤10cm), and Twigs
(<2cm). Variations of this classification scheme have been used frequently in primate positional behavior studies (e.g., Morbeck, 1977; Doran, 1993; Garber and Pruetz, 1995; McGraw, 1996a; Youlatos 1999). However, visually determining whether a support is 8cm or 12cm at heights in excess of 30m can be challenging. Instead, these categories are often used as rough size estimates based on the relationship of the support to the animal using it. For example, McGraw (1996a) differentiated Boughs from Branches based on the ability of the primate to effectively grasp the support with its hands and feet.

I also employed three additional support type categories: Trunk, Vine, and Ground. Using Moffett’s (2000) attempt at standardizing canopy biology terms, I refer to a Trunk as “a single..., erect, columnar, often woody plant axis of substantial height” (p. 578). Trunks were differentiated from Boughs because they were more associated with lower forest strata, tended to be vertical in orientation, and, at least for large trunks, were not usually found in close proximity to arboreal food resources such as fruits, seedpods, or leaves. The Vine category was recorded only when a monkey used a flexible liana-like support that was anchored at a minimum of two ends. These rope-like supports shared some of the same challenges of balance and stability with other thin, flexible supports (i.e., Twigs) but the multiple anchors of vines made these supports distinct enough to warrant a separate category. All terrestrial supports were recorded as Ground.

All support categories used in this study are listed and defined in Table 5.3 and the difference between Boughs, Branches and Twigs illustrated in Figure 5.3.
<table>
<thead>
<tr>
<th>Support Type Categories</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground</td>
<td>Terrestrial support</td>
</tr>
<tr>
<td>Trunk</td>
<td>Usually vertical, woody supports of large or medium sized trees from the ground up to the first divergent branches</td>
</tr>
<tr>
<td>Bough</td>
<td>Large arboreal supports incapable of being grasped</td>
</tr>
<tr>
<td>Branch</td>
<td>Small but inflexible arboreal supports capable of being grasped</td>
</tr>
<tr>
<td>Twig</td>
<td>Flexible terminal branches that can be grasped but are too small to support body weight without deforming substantially</td>
</tr>
<tr>
<td>Vine</td>
<td>Flexible, rope-like supports anchored at a minimum of two ends</td>
</tr>
</tbody>
</table>

**Table 5.3: Support Type Categories.**

---

**Figure 5.3: Boughs, Branches, and Twigs Illustrated.** These three photos demonstrate three of the support types used in this study. The upper left photo shows a guenon on a Bough. Note the palmigrade locomotion (i.e., her palm is falling flat atop the large support). The upper right photo shows a guenon on a Branch with hands and feet grasping the support. The lower center photo shows a guenon on Twigs distributing weight across several different terminal branch supports.
Support Orientation

The orientation of a support influences a primate’s postural and locomotor options (Garber and Preutz, 1995), the forces generated by locomotion from or onto those supports (Demes et al., 1995) and the biomechanical relationships associating positional behavior and functional anatomy (Garber and Preutz, 1995; Demes et al., 1995). This is most apparent when one contrasts the two extremes of orientation. A primate on a vertical support has a different range of postural options for resting (e.g., clinging vertically or horizontally) and locomotor options for travel (e.g., leaping, climbing, or descending vertically) than does a primate on a horizontal support. Even when the angle of orientation does not negate the possibility of using a particular locomotor or postural behavior (e.g., lie on a vertical support), there is some evidence that primates display postural or locomotor tendencies/preferences associated with a support orientation. For example, Morbeck (1977) showed that the black-and-white colobus C. guereza tends to lie on oblique rather than horizontal supports and clings almost exclusively to vertical supports.

The categories employed here parallel those used by Garber and Pruetz (1995) with two additions. While terrestrial supports tended to be horizontal, both colobus and guenons would occasionally rest and move on terrestrial inclines approaching what might otherwise be considered oblique (i.e., hill slopes). Without a horizontal plane to compare them to, these steep terrestrial grades were challenging to categorize as either horizontal or oblique. Therefore, all terrestrial supports were recorded as Ground.
Supports that were highly flexible were given their own category. Such supports changed orientation dramatically depending on how a focal animal distributed its weight across them and the nature of the resulting deformation made categorizing support angles for these substrates difficult. As such, the support orientation for all Twig-sized supports was recorded as Twigs rather than given a separate support orientation.

The categories used in this study are listed and defined in Table 5.4.

<table>
<thead>
<tr>
<th>Support Orientation Categories</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground</td>
<td>Terrestrial supports</td>
</tr>
<tr>
<td>Horizontal</td>
<td>Arboreal supports that ranged from 0°-15° from a horizontal ground plane</td>
</tr>
<tr>
<td>Oblique</td>
<td>Arboreal supports exceeding 15° and less than 75° from a horizontal ground plane</td>
</tr>
<tr>
<td>Vertical</td>
<td>Arboreal supports exceeding 75° from a horizontal ground plane</td>
</tr>
<tr>
<td>Twigs</td>
<td>Arboreal supports that deformed greatly while supporting the focal animal’s weight</td>
</tr>
</tbody>
</table>

Table 5.4: Support Orientation Categories. The range of degrees characterizing each orientation category are based on Garber and Pruetz (1995).

Results

For both *C. vellerosus* and *C. campbelli lowei*, I identified significant intraspecific variation in the use of forest strata and the use of supports of differing sizes and orientations (Table 5.5). Each of these intraspecific contrasts is detailed below.
<table>
<thead>
<tr>
<th>Species</th>
<th>Support Height</th>
<th>Support Size</th>
<th>Support Orientation</th>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. vellerosus</em></td>
<td>125.376; p&lt;0.001</td>
<td>87.482; p&lt;0.001</td>
<td>52.390; p&lt;0.001</td>
<td>Wawa Colobus: n=4901</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Redtail Colobus: n=4494</td>
</tr>
<tr>
<td><em>C. campbelli lowei</em></td>
<td>22.419; p&lt;0.001</td>
<td>62.728; p&lt;0.001</td>
<td>60.442; p&lt;0.001</td>
<td>Central Guenon: n=4613</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Periphery Guenon: n=3721</td>
</tr>
</tbody>
</table>

Table 5.5: Statistical Comparisons of Habitat Usage Profiles. G-test statistics for R x C comparisons are listed above each probability.

Support Height (Table 5.6; colobus: Figure 5.4; guenons: Figure 5.5)

Both colobus groups were observed most frequently at heights in excess of 10m but differed in their overall forest strata profiles. Female colobus in less disturbed western forest (Wawa Colobus) exhibited a clear preference for the upper canopy (47.7%) and used the lower canopy much less frequently (29.7%). In contrast, female colobus living in the more disturbed southern forest (Redtail Colobus) used the two highest forest strata (10–15m and 20m+) at similar frequencies (~35%). Both groups used terrestrial supports very rarely (<3%).

For both guenon groups, the understory was used more frequently than other forest strata (≥50%). However, the greatest frequency difference between guenon groups was found in their respective use of the understory and upper canopy. In the more disturbed southern forest, Periphery Guenon females used understory supports at a higher frequency (53.2%) than did Central Guenons (50%). In contrast, Central Guenons in the less disturbed western forest exhibited a higher frequency of upper canopy use (19.2%) than did the Periphery Guenons (15.8%). Both groups used terrestrial supports and lower canopy supports at roughly equivalent frequencies.
<table>
<thead>
<tr>
<th>Female Colobus</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m - 15m</th>
<th>20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>2.6%</td>
<td>20.0%</td>
<td>29.7%</td>
<td>47.7%</td>
<td>4901</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>2.4%</td>
<td>25.3%</td>
<td>35.8%</td>
<td>36.5%</td>
<td>4494</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Female Guenons</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m - 15m</th>
<th>20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>2.5%</td>
<td>50.0%</td>
<td>28.3%</td>
<td>19.2%</td>
<td>4613</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>3.3%</td>
<td>53.2%</td>
<td>27.7%</td>
<td>15.8%</td>
<td>3721</td>
</tr>
</tbody>
</table>

Table 5.6: Female Colobus and Guenon Forest Strata Profiles.

Figure 5.4: Comparison of Female Colobus Forest Strata Use.
Support Size (Table 5.7; colobus: Figure 5.6; guenons: Figure 5.7)

Female colobus in both forests used Boughs at a higher frequency than any other support size category followed by Branches. For Redtail Colobus, the difference between their use of Boughs and Branches (52.5%:37.4%) was greater than that for the Wawa Colobus group (49.7%:43.2%). No other support types comprised greater than 7% of all observations. However, Redtail Colobus used Twigs at a nearly twice the frequency than did the Wawa Colobus group (6.8% vs. 3.5%).

All female guenons used Branches at higher frequencies than Boughs, and Boughs and Branches collectively comprised more than 80% of all observations in both guenon groups. Periphery Guenons in more disturbed southern forest used Twigs in 10% of total observations. In contrast, female Central Guenons used Twigs
at a frequency of 6\% in the less disturbed western forest. Neither guenon group used Trunks, Vines or terrestrial supports frequently.

<table>
<thead>
<tr>
<th></th>
<th>Ground</th>
<th>Trunk</th>
<th>Bough</th>
<th>Branch</th>
<th>Twig</th>
<th>Vine</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Female Colobus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wawa Colobus</td>
<td>2.6%</td>
<td>0.9%</td>
<td>49.6%</td>
<td>43.2%</td>
<td>3.5%</td>
<td>0.2%</td>
<td>4901</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>2.4%</td>
<td>0.4%</td>
<td>52.5%</td>
<td>37.4%</td>
<td>6.8%</td>
<td>0.5%</td>
<td>4494</td>
</tr>
<tr>
<td><strong>Female Guenons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Guenons</td>
<td>2.4%</td>
<td>1.4%</td>
<td>38.7%</td>
<td>50.1%</td>
<td>6.0%</td>
<td>1.4%</td>
<td>4613</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>3.3%</td>
<td>1.6%</td>
<td>36.6%</td>
<td>46.6%</td>
<td>10.3%</td>
<td>1.9%</td>
<td>3721</td>
</tr>
</tbody>
</table>

**Table 5.7: Female Colobus and Guenon Support Type Profiles.**

**Figure 5.6: Comparison of Female Colobus Support Type Profiles.**
Figure 5.7: Comparison of Female Guenon Support Size Profiles.

Support Orientation (Table 5.8; colobus: Figure 5.8; guenons: Figure 5.9)

Females in both forests exhibited similarities in their overall pattern of support orientation preference. For example, both colobus and both guenon groups used horizontal supports in more than 60% of all observations. Neither species used terrestrial or vertical supports in excess of 5% of total observations in either forest type. It is notable, however, that the Redtail Colobus and Periphery Guenon groups living in more disturbed southern forest used Twigs at a higher frequency and horizontal supports at a lower frequency than did their counterparts in less disturbed western forest.
<table>
<thead>
<tr>
<th>Female Colobus</th>
<th>Ground</th>
<th>Horizontal</th>
<th>Oblique</th>
<th>Vertical</th>
<th>Twig</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>2.6%</td>
<td>75.5%</td>
<td>16.9%</td>
<td>1.5%</td>
<td>3.5%</td>
<td>4901</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>2.4%</td>
<td>72.6%</td>
<td>16.7%</td>
<td>1.5%</td>
<td>6.8%</td>
<td>4494</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Female Guenons</th>
<th>Ground</th>
<th>Horizontal</th>
<th>Oblique</th>
<th>Vertical</th>
<th>Twig</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>2.4%</td>
<td>68.2%</td>
<td>20.1%</td>
<td>3.3%</td>
<td>6.0%</td>
<td>4613</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>3.3%</td>
<td>62.9%</td>
<td>19.8%</td>
<td>3.7%</td>
<td>10.3%</td>
<td>3721</td>
</tr>
</tbody>
</table>

Table 5.8: Female Colobus and Guenon Support Orientation Profiles.

Figure 5.8: Comparison of Female Colobus Support Orientation Profiles.
Discussion

Habitat disturbance can substantially alter a primate’s access to food resources and may result in reduction of population densities for primates with patchily distributed diets, particularly frugivores (Johns and Skorupa, 1987). Some studies have shown, however, that primates are resistant to habitat disturbance as long as enough dietary diversity remains in their fragmented ranges (Mammides et al., 2008). In this chapter, I tested whether habitat disturbance in southern forests at BFMS (see chapter 3) was sufficient to produce significant intraspecific variation in habitat usage profiles for *C. vellerosus* and *C. campbelli lowei*. Colobus and guenon home ranges in unlogged western forest exhibited a more enclosed canopy and more large trees than did the highly disturbed southern forest. Additionally, the understory, though dense throughout BFMS, differed greatly in southern and

Figure 5.9: Comparison of Female Guenon Support Orientation Profiles.
western forest. The southern forest understory was dominated by tall heaps of vinetangled vegetation while the western forest understory was dominated by thickets of thin saplings. The different architectural features of these two forest areas likely played a role in the support and forest strata choices of colobus and guenon females living there.

Habitat usage data at BFMS indicate that the upper canopy (Stratum IV: 20m+) was used to different extents by the two monkey species. Some studies have shown associations between body size and forest strata use with smaller-bodied primates tending to be found at lower forest heights (e.g., Youlatos, 1999). This was true at BFMS as well. The upper canopy was the most frequently used forest stratum for both colobus groups but the least used arboreal stratum for both guenon groups. Body size also predictably influenced support use profiles. Theoretically, larger-bodied primates should have access to a smaller subset of supports in any given forest than do smaller-bodied primates (Fleagle, 1985). When one excludes primates with adaptations associated with clinging to or climbing on large, vertical supports [i.e., claws in tamarins (Garber and Pruetz, 1995; Youlatos, 1999)] or those associated with suspensory locomotion [e.g., prehensile tails in atelids (Fontaine, 1990; Gebo, 1992)], there exists a general association between increased body size and reduced use of small supports (Fleagle and Mittermeier, 1980; Doran, 1993; McGraw, 1996a). This was also found to be true at BFMS. *C. vellerosus* females were larger than *C. campbelli lowei* females (Delson et al., 2000) and used both Branches and Twigs at a lower frequency than did *C. campbelli lowei*. 

119
Nevertheless, predictions that one or both species at BFMS would remain conservative in their habitat usage profiles were not supported. Rather, forest strata and support characteristic profiles for both species were altered significantly in disturbed southern forest. Interestingly, intraspecific differences in the frequencies in each species’ habitat usage profiles shared some similarities between forest types. Both monkey species exhibited lower frequencies of upper canopy use in southern forest (Redtail Colobus and Periphery Guenons) than did conspecifics in less disturbed western forest (Wawa Colobus and Central Guenons). For Redtail Colobus in southern forest, reduced used the upper canopy was complemented by an increased use of both lower arboreal strata (Stratum III: 10m–15m, Stratum II: ≤5). Periphery Guenons in this same forest used the forest understory (Stratum II: ≤5) and the ground (Stratum I) at slightly higher frequency than did Central Guenons.

Cannon and Leighton (1994) argued that a primate’s tendency to be found in a particular forest stratum is negatively correlated with the number of canopy gaps found in that stratum that a primate cannot safely cross. In some cases, primates might even avoid forests in which the presence of too many gaps prevents them from foraging efficiently (Rodman, 1991). At BFMS, the southern forest consisted of a mosaic of narrow primary tree corridors surrounding largely open areas of previously cleared forest. Corridors of primary trees provided arboreal pathways that both species could utilize, but patches of cleared forest may have extended the length of upper canopy pathways across segments of each group’s home range.
The greater number of large trees and more intact upper canopy found in western, unlogged forest likely provided numerous direct pathways across the respective ranges of the colobus and guenons found there. This may not have been the case in the southern forest where following upper canopy arboreal pathways might have taken guenons and colobus along more circuitous and indirect routes. On occasion, by descending to lower strata in disturbed southern forest, guenon and colobus females may have been able to travel more directly across their respective ranges. Primates are expected to minimize energy expenditures by traveling as directly as possible while factoring in the location of potential food items and the risks of predation (Cant and Temerin, 1984; Cant, 1992). It is possible that colobus and guenons in more disturbed southern forest would have made use of direct paths located in the forest understory or lower canopy more frequently than conspecifics in more intact western forest.

Another possible explanation for increased use of lower forest strata by both species is that the less interconnected upper canopy in southern forest offered fewer food resources than could be found in the more intact and abundant upper canopy of unlogged western forest. How a primate adapts its foraging strategies to respond to habitat disturbance is a complex problem influenced by numerous variables including distribution of preferred foods, body size, predation risk, human/monkey conflict, etc. [see Johns and Skorupa (1987) for a review]. Measuring the effect of habitat disturbance on a primate’s dietary tendencies is even more challenging because it requires substantial knowledge of the diversity of foods
a primate is likely to eat, the distribution of those foods and their relative nutritional qualities (Mammides, 2008). Some monkey species have been shown to thrive (usually inferred from increased population density) in the face of habitat loss and disturbance, as long as they have access to adequate food diversity (Mammides, 2008). Other species substantially alter their habitat usage under conditions of habitat disturbance. For example, Siemers (2000) found that the brown capuchin (Cebus apella) in highly disturbed and fragmented forest made use of lower forest strata during portions of the year when preferred upper canopy food resources were less available.

Detailed dietary data collected in future studies are needed to confirm any increased dietary stress in southern forests at BFMS. However, if the fewer and more patchily distributed large trees of southern forest offered less food in the upper canopy strata than was available in lower forest strata, any number of food resources located in lower strata (i.e., alternate leaves in vine heaps or periphery of lower canopy trees for colobus; alternate insect resources, larva, and low-hanging fruit for guenons) or on the ground (e.g., fallen fruit, discarded human food) might also have enticed colobus and guenons to these lower heights.

The use of lower forest strata by both colobus and guenons at BFMS may explain the differing support size and orientation profiles exhibited by females in the two forest types. Many arboreal food resources (e.g., leaves, seedpods, fruits) tend to be found in association with thin supports (Cant, 1992). The location of frequently consumed food items therefore influences support size profiles (McGraw,
Redtail Colobus and Periphery Guenons living in southern forest used Twigs (e.g., thin, flexible supports) at a higher frequency than did females of the same species in western forest. Because Twigs served as a common category for both support size and support orientation, the increased use of Twigs in southern forest affected the overall profiles for both of these support characteristics. For Redtail Colobus, increased Twig use was accompanied by decreased use of Branches and Horizontal supports. For Periphery Guenons, increased Twig use was accompanied by decreased use of Branches and Boughs as well as Horizontal supports.

Regardless of why colobus and guenons in southern forest used lower forest strata more frequently than those in western forest, the reduced availability of large supports found there likely influenced support type profiles for both species. McGraw (1996a) reported that disturbed areas of the Tai Forest, Cote d’Ivoire were characterized by a greater number of total supports and, in low strata, a higher proportion of thin supports (Branches and Twigs). Though I did not collect data on the total number or relative proportion of supports of different types at BFMS, both understory and lower canopy strata also included numerous thin supports and few large supports. This was particularly true for the southern forest understory where tangled vines wrapped themselves in undulating, vine heaps around broken saplings and larger trunks. These heaps were dominated by tightly woven, thin, flexible supports (mostly Twigs but branches as well) over which Redtail Colobus rested their body mass while feeding on leaves (i.e., attached to vines or the branches of
nearby saplings) and within which guenons foraged for fruit and insect prey.

Therefore, the nature of the understory and lower canopy in southern forest was such that as monkeys moved along arboreal pathways or foraged in these strata, they were more likely to encounter and choose to use thin, flexible supports.

Many researchers have argued that the association between forest strata and the nature of the supports likely to be found there greatly influence primate positional behavior (Fleagle and Mittermeier, 1980; Morbeck, 1977; Doran, 1993; McGraw, 1996a; Youlatos, 1999). The fact both colobus and guenons in this study varied their support usage profiles suggests the possibility that they might also have altered their positional behavior. Of course, we cannot assume that intraspecific support usage differences will necessarily lead to differences in positional behavior. For example, Garber and Pruetz (1995) showed that groups of moustached tamarin (Sanguinus mystax) living in two different forest types did exhibit differing profiles of support use (i.e., size and orientation) but did not differ significantly in their patterns of positional behavior. The nature of habitat use and forest differences at BFMS offers an ideal opportunity to further test the conservative nature of primate positional behavior on two species that differ in terms of diet, morphology and socioecology.

**Summary**

In this chapter, I tested for intraspecific differences in habitat use for groups of *C. vellerosus* and *C. campbelli lowei* inhabiting two forest areas characterized by
differing levels of anthropogenic disturbance. Using data collected from instantaneous focal sampling on adult females of both species, I tested whether groups living in unlogged western forest differed in their use of forest strata as well as their use of supports with differing characteristics (i.e., different sizes and orientations). I considered these comparisons in the context of forest canopy and understory contrasts described in Chapter 3. These tests produced the following results:

1. Female colobus and guenons from groups in the two forests at BFMS differed in their overall use profiles for support characteristics (size and orientation) and forest strata (vertical distribution of used supports).

2. Both monkey species in mosaic southern forest used low and thin supports at greater frequencies than did their counterparts in less disturbed western forest.

3. The less intact upper canopy in disturbed southern forest likely reduced the number of direct pathways between distant points within each group’s home range and may have offered fewer food resources than could be found in western forest upper canopy. Either or both of these factors may have contributed to the increased use of lower strata by guenon and colobus groups living in southern forest.
4. I suggest that a greater proportion of Branches and Twigs were encountered by both monkey species in low canopy and in the dense, vine-tangled understory of southern forest. Higher frequencies of Twig use in southern forest for both monkey species were therefore associated with increased use of lower strata and lower frequencies of large and horizontal support use.

In the following chapters, I test whether differences in forest structure and support usage are sufficient to cause *C. vellerosus* and/or *C. campbelli lowei* to alter their positional behavior profile.
Chapter 6: Intraspecific Differences in Posture

Introduction

Prost (1965) noted that a primate's positional repertoire is comprised of two classes of behavior: posture and locomotion. These behavioral states are not a true dichotomy but rather lie on a spectrum of body movement separated by a theoretical threshold. Posture refers to body orientations that fall below this threshold and include periods when a primate's body is at complete rest (i.e., no discernable movement) as well as when its body exhibits only minor shifts in mass (e.g., arm movements, repositioning of legs, swaying of the body). Researchers have previously examined positional behavior in the context of these two behavioral states (e.g., Morbeck, 1977; Fleagle, 1980; Fontaine, 1990; Garber, 1991; McGraw, 1996; Johnson and Shapiro, 1998; Thorpe and Crompton, 2006).

Postural behaviors tend to lack the element of spectacle associated with exciting and often loud locomotor behaviors (e.g., crashing through the forest canopy). Nevertheless, postural behaviors have likely played a significant role in shaping primate evolutionary history and behavioral diversity. Rose (1974) suggested that primates, throughout their waking period, employ postures more frequently than locomotor behaviors. Because of their frequency and the fact that they often mark transitions between different locomotor states (i.e., quadrupedal
run to the edge of a bough, stand while selecting arboreal pathways, and then leaping), postures may be just as significant in understanding a primate’s socioecology as its locomotor behaviors (Rose, 1974; McGraw, 1998b). As a result, many examples of morphological variation across primate taxa might be as correlated with postural differences as they are with locomotor differences. For instance, Rose (1974) noted that: 1) bipedalism and its associated morphological adaptations may be as closely tied to postural activities (i.e., standing and reaching foods, scanning above grasses) as locomotor activities for most terrestrial monkeys; 2) long, prehensile tails for large-bodied New World monkeys might be as tied to balance while standing above arboreal supports or suspending below supports as they are useful as a locomotor tool; and 3) claws may have evolved in the small-bodied callitrichidae as much to anchor them to vertical supports while feeding as they do in climbing those supports. Data on posture in combination with data on locomotion, therefore, provide two vital components in explaining variation in primate morphology, habitat use, and foraging decisions.

In Chapter 3, I compared the forest habitats of two study groups of *C. vellerosus* and *C. campbelli lowei*. I found that these forests differed in canopy density and exhibited similarly dense though structurally distinct understories. In Chapter 5, I tested for and identified a dependent relationship between forest type and the use of different supports and forest strata by both colobus and guenons. I argued that contrasting forest architectures (i.e., canopy density and the nature of southern forest understory) were a driving factor differentiating forest strata
profiles for each species and by association the frequencies at which they used supports of differing sizes and orientations. In this chapter, I test whether this architectural variation was sufficient to produce significantly different postural profiles between colobus and guenon groups at BFMS.

**Hypotheses**

- **Research Question**: Do the overall postural profiles of colobus and guenons living in more intact western forest at BFMS differ from the postural profiles of the same species living in more disturbed southern forest?

Given differences in forest architecture and support usage already identified for both species at BFMS, I make the following predictions regarding intraspecific postural variation summarized in Table 6.1. Postural behaviors recorded in this study are defined in this chapter’s methods section in Table 6.5.

<table>
<thead>
<tr>
<th>Predictions</th>
<th>Intraspecific Postural Differences</th>
<th>Cause</th>
<th>Type of Change in More Disturbed Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H_0$</td>
<td>No change for either species</td>
<td>Morphological constraints</td>
<td>No change; statistically similar postural profiles</td>
</tr>
<tr>
<td>$H_1$</td>
<td>Both species change</td>
<td>Availability of weight-bearing supports</td>
<td>Reduction in <em>Recline</em> postures</td>
</tr>
</tbody>
</table>
| $H_2$       | Change in guenons but not colobus  | Combined effects of body size and the availability of preferred food items | -Colobus: No change  
- Guenons: Reduction in *Recline* and *Sit* postures; increase in *Stand* postures |

**Table 6.1: Predictions for Intraspecific Variation in Postural Profiles.**
Based on results from previous studies comparing primate positional behavior in different forest habitats (e.g., Doran and Hunt, 1994; Garber and Pruetz, 1995; McGraw, 1996a), H₀ predicts that postural profiles remained conservative between study groups of the same species found in different forest types at BFMS. In other words, neither female *C. vellerosus* nor female *C. campbelli lowei* will have exhibited significant intraspecific differences in postural profiles. Though support use was found to vary between groups in this study, this hypothesis predicts that both monkey species in more disturbed habitat nevertheless selected those supports upon which they were capable of ensuring postural continuity.

H₁ predicts that forest differences at BFMS are sufficient to produce changes in both monkey species’ postural profiles. In more disturbed southern forest, both species were found to use supports in the upper canopy less frequently and use supports in at least one of the two lower arboreal strata more frequently than their counterparts in less disturbed forest. Both monkey species also used Twigs (thin, flexible supports) more frequently in southern forest. H₁ predicts that the increased use of Twigs by Redtail Colobus in southern forest, would require alterations of their postural profiles in order to maintain stability and balance. For example, black-and-white colobus often lie on large, oblique supports (Morbeck, 1977). *Recline* postures might have been impractical on these thin supports and therefore the frequency of these postures reduced in southern forest. Further, black-and-white colobus rarely *Stand* but *Sit* frequently (McGraw, 1998b). McGraw (1998b) discussed several possible explanations for such high rates of *Sit* including
temperature regulation, energy conservation, and the distribution of preferred food items. In southern forest at BFMS, *Sit* postures might allow colobus to distribute their weight across many flexible supports in a more controlled manner than do *Recline* postures. Southern forest guenons (Periphery Guenons) used the understory at higher frequency than did guenons in unlogged, western forest. Guenons do frequently *Stand* and use this posture to actively scan for high competition food resources (McGraw, 1998b). As such, $H_1$ predicts that Periphery Guenons exhibit higher frequencies of *Stand* and *Sit* but lower frequencies of *Recline* postures that might be harder to maintain atop the flexible and densely interwoven vegetation dominating southern forest understory.

$H_2$ predicts that differences in body size and diet between the study species influence the nature of intraspecific postural variation at BFMS (Table 6.2). Past studies characterized the larger-bodied (Delson et al., 2000) ursine colobus as highly folivorous and have noted that leaves comprise nearly the entirety of their diet for large segments of the year when other food resources become unavailable (Saj et al., 2005; Saj and Sicotte 2007a). Lowe’s monkeys at BFMS are known anecdotally to feed most frequently on insects, fruits, and scavenged foods (Fargey, 1992, personal observation). Quantitative dietary data for its close phylogenetic relative (*C. campbelli campbelli*) in the Tai Forest, Cote d’Ivoire, support this high degree of insectivory/frugivory (Buzzard, 2006).
Table 6.2: Diet and Body Mass of *C. vellerosus* and *C. campbelli lowei*. Body masses were reported in Delson et al. (2000). *C. vellerosus* dietary data were collected from colobus at BFMS and were reported in Saj et al. (2005). *C. campbelli lowei* diets are inferred data collected by Buzzard (2006) on its sister taxon *C. campbelli campbelli*.

H₂ predicts that Redtail Colobus in disturbed southern forest are likely more conservative in their postural profiles (i.e., no significant difference in postural profiles between forests) than are guenons. Because leaves (particularly mature leaves) tend to be less patchily distributed than many other food sources (e.g., fruits, insects) and are often distributed in bunches within tree crowns (Garber, 1987; Oates, 1987), leaf-eaters are capable of “banquet” feeding (i.e., feeding continuously in a single location for long periods of time with only limited movement between feeding sites) (Oates, 1987). A folivorous diet has been associated with high rates of *Sit* (i.e., during feeding bouts) and *Recline* (i.e., during digestion) for other black-and-white colobus species (McGraw, 1998b). Due to the relative ease with which colobus might be able to find less patchily distributed preferred food items than can guenons, H₂ predicts that Redtail Colobus are better able to meet their dietary demands in the mosaic upper canopy than Periphery Guenons (i.e., the forest strata that both colobus groups use at the highest frequency—see Chapter 5). While
support choices differed between colobus females in western and southern forests, Redtail Colobus may select similar enough supports (i.e., those comfortable and strong enough to balance/bear their weight) as those selected by Wawa Colobus in unlogged western forest during activities typically associated with postural behavior (e.g., feeding, resting). In other words, there might be little cause to alter preferred posture because the ecological contexts in which associated activities occur might not differ substantially.

Oates (1987) argued that competition over fruit and non-social insect resources is likely higher than competition over leaves because of their more patchy distribution. Therefore, H2 predicts that, due to their more competitive diet of fruits and insects, Periphery Guenons in more disturbed southern forest alter their postural profiles significantly when compared to Central Guenons in less disturbed western forest. McGraw (1998b) noted that guenons tend to stop and feed repeatedly while traveling and employ postures that facilitate rapid movement toward desired food items. Since Periphery Guenons were found in the understory more frequently than Central Guenons, H2 predicts that Periphery Guenons use postures that facilitate movement through and foraging within this stratum. Understory supports may be too weak and/or too flexible to support an individual’s full body weight. On small supports, Stand may offer females better balance through greater control of how they distribute their weight (e.g., hands grasping four supports rather than body weight across multiple supports). Additionally, if insect or fruit resources are sought out more frequently in southern forest understory
than they are in western forest understory, *Stand* would have graded easily into locomotor behaviors like *Leap* or *Horizontal Climb* that could have been used to quickly acquire these high competition food items.

**Methods**

I collected frequency data on the postural behavior of *C. vellerosus* and *C. campbelli lowei* using a three-minute instantaneous focal sampling method. The postural behavior of each species was recorded in two forest areas characterized by different degrees of anthropogenic disturbance. To avoid any confounding affects that sex-differences may have on these data, only females are included in this chapter for purposes of postural comparison. Sex differences in posture are examined in Chapter 8.

At each three-minute time point I recorded the following information:

- Sex
- Support Characteristics: Size and Orientation
- Forest Stratum
- Maintenance Activity
- Postural Behavior

I classified the maintenance behavior associated with each focal animal’s posture into one of five categories (Table 6.3). In this chapter, I compare overall postural profiles (i.e., the number of observations of a particular posture) between study groups in less disturbed and more disturbed forests. I also compare groups
while controlling for maintenance activity in order to better understand which activities may be contributing most greatly to intraspecific postural differences.

<table>
<thead>
<tr>
<th>Postural Maintenance Activities</th>
<th>Definition</th>
<th>Examples</th>
</tr>
</thead>
</table>
| Active Feed                     | Direct consumption of food items at the site where those food items were acquired | - Eating leaves from branches  
- Eating insect larva from the bottom of leaves |
| Food Processing/ Acquisition    | Manual processing of environment to access a potential food item or the processing of a food item to facilitate consumption | - Ripping bark to find insects  
- Flipping leaves to look for larva  
- Cleaning discarded human foods  
- Stripping yam peels |
| Rest                            | Body mass, especially the torso, is stationary; limbs or head may be moving | - Sleeping  
- Stretching limbs  
- Scanning environment |
| Rest Feed                       | Consumption of food items removed from the site where those food items were acquired | - Fruit gathered and moved to another location for consumption |
| Rest Social                     | Social activities directed by the focal animal at another group member or an extra-group individual whether affiliative or agonistic | - Open mouth or vocal threats  
- Alarm or territory calls  
- Grooming  
- Play |

**Table 6.3: Posture-Associated Maintenance Activities.** This table lists the five postural maintenance activities used in this study with definitions and examples of each category.

Following Hunt et al. (1996), I generated an extensive list of possible postural categories. This list was developed prior to this study using other positional behavior studies on comparable species as reference and adjusted based on early observations made while following members of each species. These postures are listed and defined in Table 6.4.
<table>
<thead>
<tr>
<th>Recorded Postural Categories</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bipedal Stand</td>
<td>Weight supported on hindlimbs and torso oriented vertically</td>
</tr>
<tr>
<td>Bipedal Stand w/ Forelimb Support</td>
<td>A single forelimb offers balance/support while the majority of the weight is supported by hindlimbs; torso oriented vertically</td>
</tr>
<tr>
<td>Forelimb Suspend</td>
<td>Under-branch posture with weight supported by one or both forelimbs extended above the head</td>
</tr>
<tr>
<td>Hindlimb Suspend</td>
<td>Under-branch posture with head below torso and weight supported by hindlimbs</td>
</tr>
<tr>
<td>Horizontal Cling</td>
<td>Body oriented parallel to the ground gripping the sides of a horizontal support</td>
</tr>
<tr>
<td>Back/Side Lie</td>
<td>Body weight supported by resting either the back or side of the torso directly against a substrate</td>
</tr>
<tr>
<td>Sit</td>
<td>Body weight rests on upper thighs or Ischia; torso either oriented vertically or hunched forward over legs</td>
</tr>
<tr>
<td>Sprawl</td>
<td>Body weight supported by resting the ventral surface of the torso directly against a substrate; legs extended on either side of the support</td>
</tr>
<tr>
<td>Quadrupedal Stand</td>
<td>Body weight supported on three or four limbs; pronograde torso</td>
</tr>
<tr>
<td>Vertical Cling</td>
<td>Body oriented perpendicular to the ground and is supported primarily by the hindlimbs resting against a vertical support</td>
</tr>
</tbody>
</table>

**Table 6.4: Recorded Postural Categories.** These postures were recorded during the observational portion of the study and later pooled into broad postural categories for statistical analysis.

I used Row x Column tests for independence to compare frequency tables generated for each group's overall postural profile and each group's postural profile by maintenance activity. Significant results for all tests (p<0.05) indicate a dependent relationship between column and row variables. For example, if forest type and posture were used to generate profiles for each study group, a significant result in a R x C test comparing these profiles indicate that the two profiles differed more than might be expected by chance.

During analysis, similar postures were lumped into broad postural categories. Pooled categories produced fewer columns on frequency tables and were necessary in order to avoid generating frequency tables in which more than
20% of entries had expected values <5 (minimal requirements for statistical tests—see Chapter 4; Sokal and Rohlf, 1995; McKillup, 2005). In this study, pooling data was appropriate because the broadened categories reflected similar postural strategies used to negotiate similar ecological challenges and created a dataset that facilitated the comparison of this study with other positional behavior studies (particularly McGraw, 1998a,b—see Chapter 9). In Table 6.5, I list each postural category, the postures included in each category, and a brief rationale for grouping these behaviors. The “Other” category consisted of rare behaviors (usually <10 observations). Many of the more commonly observed postures are illustrated in Appendix A.

<table>
<thead>
<tr>
<th>Lumped Postural Category</th>
<th>Postures Included</th>
<th>Ecological Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cling*</td>
<td>Horizontal Cling</td>
<td>In guenons, clings were typically associated with feeding behaviors between travels</td>
</tr>
<tr>
<td></td>
<td>Vertical Cling</td>
<td></td>
</tr>
<tr>
<td>Recline</td>
<td>Back/Side Lie</td>
<td>Both lies and sprawls were postures typically associated with prolonged rests</td>
</tr>
<tr>
<td></td>
<td>Sprawl</td>
<td></td>
</tr>
<tr>
<td>Sit</td>
<td>Sit</td>
<td>Sit is considered a baseline resting posture and was very common for all groups</td>
</tr>
<tr>
<td>Stand*</td>
<td>Bipedal Stand</td>
<td>Stand is considered an intermediate or transitional posture between other postures and/or locomotor categories</td>
</tr>
<tr>
<td></td>
<td>Bipedal Stand w/</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Forelimb Support</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quadrupedal Stand</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>Forelimb Suspend</td>
<td>Postures that occurred very rarely and were likely not critical to daily activity patterns</td>
</tr>
<tr>
<td></td>
<td>Hindlimb Suspend</td>
<td></td>
</tr>
</tbody>
</table>

*These categories were very rarely observed for colobus and were instead grouped into the “Other” category for analysis leaving only “Recline”, “Sit” and “Other” posture categories.

Table 6.5: Lumped Postural Categories. This table lists pooled postures used for statistical comparison, the recorded postures included in each and the similar ecological conditions used to justify each grouping.
**Results**

*C. vellerosus: Intraspecific Comparisons for all Postures*

When profiles for all female colobus postures are considered, posture and forest type exhibited a significantly dependent relationship (G-test: 14.537; p=0.001). Postural frequencies for each colobus group are listed in Table 6.6 and compared in Figure 6.1. In unlogged western forest, Wawa Colobus females engaged in *Sit* postures at a slightly lower frequency (87.4% vs. 90.0%) and *Recline* postures at a slightly higher frequency (12.1% vs. 9.4%) than Redtail Colobus females. Postural frequencies for these behaviors differed between colobus groups by approximately 3%. The frequencies for *Other* postures were nearly identical in the two colobus groups and comprised <1% of all observed female colobus postures for either group. As such, the differences in *Recline* and *Sit* postures likely drove overall postural differences between colobus groups.
<table>
<thead>
<tr>
<th>Group</th>
<th>Recline</th>
<th>Sit</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>12.1%</td>
<td>87.4%</td>
<td>0.6%</td>
<td>4232</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>9.4%</td>
<td>90.0%</td>
<td>0.5%</td>
<td>3886</td>
</tr>
</tbody>
</table>

**Table 6.6: Overall Postural Profiles for Female Colobus.**

![Graph showing postural profiles for Wawa Colobus and Redtail Colobus](image)

**Figure 6.1: Comparison of Overall Female Colobus Postural Profiles.**

*Figure 6.1: Comparison of Overall Female Colobus Postural Profiles.*

*C. campbelli lowei: Intraspecific Comparisons for all Postures*

When profiles for all female guenon postures are considered, posture and forest type also exhibited a dependent relationship (G-test: 14.502; p=0.006).

Postural frequencies for female Central Guenons and female Periphery Guenons are listed in Table 6.7 and compared in Figure 6.2. In unlogged western forest, the Central Guenon females engaged in the *Sit* posture at a higher frequency (80.2% vs. 77.6%) and the *Stand* posture at a lower frequency (15.2% vs. 18.6%) than did
female Periphery Guenons. Frequencies of Recline, Cling, and Other postures were comparatively low for both groups (<0.5%) and similar between both forest types.

<table>
<thead>
<tr>
<th>Group</th>
<th>Cling</th>
<th>Recline</th>
<th>Sit</th>
<th>Stand</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>1.0%</td>
<td>3.2%</td>
<td>80.2%</td>
<td>15.2%</td>
<td>0.4%</td>
<td>3154</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>0.7%</td>
<td>3.0%</td>
<td>77.6%</td>
<td>18.6%</td>
<td>0.2%</td>
<td>2428</td>
</tr>
</tbody>
</table>

Table 6.7: Overall Postural Profiles for Female Guenons.

![Figure 6.2: Comparison of Overall Female Guenon Postural Profiles.](image)

Posture by Maintenance Activity: *C. vellerosus and C. campbelli lowei*

For both monkey species, I tested for intraspecific differences in the postures used during five different maintenance activities. Table 6.8 lists the results of these comparisons. Food Processing and Rest Feed were rarely recorded for colobus and
did not provide enough data to run statistical comparisons. Rest was the only maintenance activity during which posture and forest type proved to be significantly dependent variables for either species (Fisher Exact Tests—Colobus: 24.008, p<0.001; Guenons: 17.645, p<0.001). Because there was effectively no difference in postural profiles for other activities, only those postures occurring during the Rest activity are considered in subsequent analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Active Feed</th>
<th>Food Processing</th>
<th>Rest</th>
<th>Rest Feed</th>
<th>Rest Social</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. vellerosus</td>
<td>p=0.618</td>
<td>n/a</td>
<td>p&lt;0.001</td>
<td>n/a</td>
<td>P=0.539</td>
</tr>
<tr>
<td>C. campbelli lowei</td>
<td>p=0.180</td>
<td>p=0.063</td>
<td>p&lt;0.001</td>
<td>p=0.735</td>
<td>p=0.107</td>
</tr>
</tbody>
</table>

**Table 6.8: Results of Female Postural Profile Comparisons.** Fisher Exact Tests were performed for each of these statistical comparisons with two exceptions. For colobus, Food Processing and Rest Feed comparisons were not possible because they were observed too infrequently.

**C. vellerosus: Intraspecific Postural Comparisons during the Rest Activity**

Postural frequencies for females from the Wawa Colobus and Redtail Colobus groups are listed in Table 6.9 and compared in Figure 6.3. At greater than 80% for both groups, *Sit* was the dominant posture for female colobus during the Rest activity. The use of *Other* postures was negligible (<0.5% for both groups). In unlogged western forest, Wawa Colobus females exhibited higher frequencies of *Recline* and lower frequencies of *Sit* than did Redtail Colobus females. Though the overall profile differed significantly between colobus groups, the greatest difference between groups in the frequencies of any given posture was less than 4%.
The frequencies of postures adopted during the Rest activity by female Central Guenons and Periphery Guenons are listed in Table 6.10 and compared in Figure 6.4. Approximately 80% of all Rest postures used by female guenons in both groups were Sit. Stand was the second most frequently used posture in both groups and accounted for approximately 15% of all Rest postures. The greatest intraspecific differences in Rest postures were in the frequency of Sit and Stand postures, but in both cases differences between groups was <4%. Central Guenon females in

### Table 6.9: Postural Profiles of Female Colobus during Rest.

<table>
<thead>
<tr>
<th>Group</th>
<th>Recline</th>
<th>Sit</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>15.2%</td>
<td>84.7%</td>
<td>0.1%</td>
<td>3172</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>11.3%</td>
<td>88.4%</td>
<td>0.3%</td>
<td>2918</td>
</tr>
</tbody>
</table>

### Figure 6.3: Comparisons of Rest Postural Profiles for Female Colobus.

*C. campbelli lowei*: Intraspecific Postural Comparisons during the Rest Activity

The frequencies of postures adopted during the Rest activity by female

Central Guenons and Periphery Guenons are listed in Table 6.10 and compared in Figure 6.4. Approximately 80% of all Rest postures used by female guenons in both groups were Sit. Stand was the second most frequently used posture in both groups and accounted for approximately 15% of all Rest postures. The greatest intraspecific differences in Rest postures were in the frequency of Sit and Stand postures, but in both cases differences between groups was <4%. Central Guenon females in
unlogged western forest engaged in *Sit* postures more frequently but engaged in *Stand* and *Recline* postures less frequently than did Periphery Guenon females in the more disturbed southern forest. *Clings* were uncommon in both groups (<1.5%) and only observed on 5 occasions among Periphery Guenons.

<table>
<thead>
<tr>
<th>Group</th>
<th>Cling</th>
<th>Recline</th>
<th>Sit</th>
<th>Stand</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>1.2%</td>
<td>2.8%</td>
<td>82.5%</td>
<td>13.4%</td>
<td>2249</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>0.3%</td>
<td>3.3%</td>
<td>79.4%</td>
<td>16.9%</td>
<td>1500</td>
</tr>
</tbody>
</table>

Table 6.10: Postural Profiles of Female Guenons during Rest.

![Figure 6.4: Comparisons of Rest Postural Profiles for Female Guenons.](image_url)
Discussion

In chapter 3, I demonstrated that unlogged, western forest and more disturbed, southern forest differed dramatically in some elements of forest architecture. The southern forest canopy was more open than was the western forest canopy offering and, I suggested, that there were fewer direct upper canopy pathways. Without as many upper canopy alternatives, I argued that these differences in forest architecture help explain why females of both monkey species in southern forest chose to occupy lower forest strata and to use the thin, flexible supports often found there with greater frequency than did conspecifics in less disturbed forest. These differences in forest strata and support use likely underlie the significant differences in postural profiles identified in this chapter.

There is a dependent relationship between forest type and posture for colobus at BFMS. In other words, there was a significant difference in overall postural profiles between the two colobus study groups. Since posture adopted during Rest accounted for approximately 75% of all observed colobus postures, Rest postures likely drove the broader association between posture and forest type. If differences in the use of forest strata and the typical characteristics of the supports found there drove differences in postural profiles between colobus groups, we might expect these colobus groups to differ in which strata common postures tended to occur. In Figure 6.5 and Table 6.11, I compare the vertical distribution of postures adopted during the Rest activity for Wawa Colobus in less disturbed western forest and Redtail Colobus in more disturbed southern forest.
Table 6.11: Forest Strata Profiles of Common Postures for *C. vellerosus*.

<table>
<thead>
<tr>
<th>Posture</th>
<th>Colobus Group</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m-15m</th>
<th>20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recline</td>
<td>Wawa</td>
<td>0%</td>
<td>18.4%</td>
<td>42.0%</td>
<td>39.5%</td>
<td>483</td>
</tr>
<tr>
<td></td>
<td>Redtail</td>
<td>0%</td>
<td>14.8%</td>
<td>56.4%</td>
<td>28.8%</td>
<td>330</td>
</tr>
<tr>
<td>Sit</td>
<td>Wawa</td>
<td>1.0%</td>
<td>17.8%</td>
<td>31.5%</td>
<td>49.7%</td>
<td>2687</td>
</tr>
<tr>
<td></td>
<td>Redtail</td>
<td>0.6%</td>
<td>19.0%</td>
<td>40.8%</td>
<td>39.6%</td>
<td>2560</td>
</tr>
</tbody>
</table>

Figure 6.5: Vertical Distribution of Common Postures for *C. vellerosus*.

Overall, Redtail Colobus females in more disturbed southern forest engaged in *Sit* postures approximately 4% more frequently and *Recline* postures approximately 4% less frequently than did Wawa Colobus females. Though all colobus exhibited a preference for the upper canopy, Redtail Colobus females were observed to use both the lower canopy (10–15m) and understory (≤5m) approximately 5% more often than did Wawa Colobus females (Chapter 5). Compared to Wawa Colobus females, a larger proportion of all *Sit* postures exhibited by Redtail Colobus occurred in the intermediate arboreal forest strata.
(10m–15m) while a smaller proportion of *Recline* postures occurred at the highest arboreal strata (20m+). These comparisons suggest that Redtail Colobus females engaged in *Sit* postures more frequently and *Recline* postures less frequently than did Wawa Colobus females. Further, the contrast between colobus groups was associated with increased use of the lower canopy by Redtail Colobus.

In Chapter 5, I argued that colobus in disturbed southern forest may, at times, have chosen to exploit arboreal pathways not found in the upper canopy because lower routes provide a more direct path between locations. This was a consequence of the mosaic nature of the southern forest. Corridors of primary forest trees are not available everywhere within the Redtail Colobus home range and alternate routes may have been preferred for any number of reasons (e.g., to facilitate quick movement from one point to another, to access alternative food resources). In fact, it was not uncommon for colobus to descend to the forest floor and travel along streambeds or trails to quickly move across their range, to avoid approaching humans, or to access understory vegetation. Outside of the village, colobus rarely stayed on the ground for long. Instead, they tended to move back up into the understory as soon as they encountered a desired food item or were approached by human observers.

Large boughs tend to be found in higher frequency in the upper canopy than in lower forest strata at BFMS (McGraw, 1996a). Black-and-white colobus have been shown to prefer these large supports for Resting behavior (Morbeck, 1977; McGraw 1998b). Further, large-bodied folivorous primates like *C. vellerosus* that frequently
engage in Quadrupedalism may preferentially select large, horizontal boughs found high in the canopy because they facilitate crossing their range quickly and allow access to thinner supports in the periphery of tree crowns where desired leaf resources might be found (Cant, 1992; McGraw, 1998b). Should a large-bodied primate find itself in a position where large supports are unavailable or the use of large supports would not achieve its desired goal (e.g., feeding on the leaves of a small sapling outside the reach of larger adjacent trees), they might still be able to access those resources by distributing their body mass across multiple thin supports. At least one study has shown that increased use of multiple supports did correlate with increased primate body size (Fontaine, 1990).

While I did not differentiate single from multiple supports in this study, the increased use of Twigs by colobus in southern forest was typically associated with the use of multiple supports (Figure 6.6). Thin supports comprised much of dense heaps of vegetation covering dead saplings in southern forest understory. When in the understory, colobus would typically rest along the outer edge of these heaps of vegetation. Similarly, in the lower canopy, where colobus Sit postures were more frequent, females would often distribute their weight across numerous thin supports in the periphery of tree crowns. Sit postures may have been more suited to both of these environments than were Recline postures. Sit postures may include a variety of body orientations (Hunt et al., 1996; McGraw, 1998). For example, colobus at BFMS adopted subtly different postures when sitting that included: 1) sitting with legs extended across additional supports; 2) sitting with legs retracted and the
trunk hunched forward; and 3) sitting with the back resting against a vertical support. This variability allowed the female colobus to make use of adjacent large boughs or trunks for additional support (i.e., rest a portion of their weight against more stable supports), to adjust the orientation of her limbs to maintain balance and/or to anchor her weight by grasping onto many available supports. In contrast, colobus in the Recline posture typically rested the majority their body mass against a single primary support, rarely grasping additional nearby supports to maintain balance. Increased rates of Sit in southern forest, I argue, is best explained by Redtail Colobus’ increased use of the lower canopy and their attempt to maintain balance and prevent support collapse on the thin, flexible supports found there.

Figure 6.6: Twig-Associated Sit Postures for C. vellerosus. In the disturbed southern forest understory (≤5m), colobus tended to sit on top or along the side of massed vegetation and distribute their weight across numerous flexible supports (left photo). In the lower canopy, when large supports were unavailable or inconvenient colobus would more often distribute their weight across multiple flexible supports (right photo).

Guenon groups also exhibited a dependent relationship between forest type and posture at BFMS. Periphery Guenons used Sit postures less frequently and Stand
postures more frequently than did Central Guenon females. In Chapter 5, I found that both guenon groups used the forest understory at least 20% more frequently than they did any other forest strata. Though frequencies differed between guenon groups by only 3%, Periphery Guenons were observed to use the understory (≤5m) more frequently and the upper canopy (20m+) less frequently than did Central Guenons. Use of the lower canopy (10m–15m) was nearly identical between the two groups. If intraspecific differences in the use of forest strata drove differences in postural profiles between guenon groups, then those postures that saw increased use in the understory of southern forest might best explain these postural contrasts.

In Figure 6.7 and Table 6.12, I compare the frequency of different postures adopted during Rest by females from both guenon groups for each of the four forest strata recognized in this study.

<table>
<thead>
<tr>
<th>Posture</th>
<th>Guenon Group</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m-15m</th>
<th>20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cling</td>
<td>Central</td>
<td>0%</td>
<td>81.5%</td>
<td>14.8%</td>
<td>3.7%</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Periphery</td>
<td>0%</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
<td>5</td>
</tr>
<tr>
<td>Recline</td>
<td>Central</td>
<td>0%</td>
<td>59.4%</td>
<td>37.5%</td>
<td>3.1%</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>Periphery</td>
<td>2%</td>
<td>48%</td>
<td>28%</td>
<td>22%</td>
<td>50</td>
</tr>
<tr>
<td>Sit</td>
<td>Central</td>
<td>1.1%</td>
<td>56.6%</td>
<td>29.7%</td>
<td>12.6%</td>
<td>1856</td>
</tr>
<tr>
<td></td>
<td>Periphery</td>
<td>1.5%</td>
<td>58.1%</td>
<td>25.9%</td>
<td>14.5%</td>
<td>1191</td>
</tr>
<tr>
<td>Stand</td>
<td>Central</td>
<td>3.6%</td>
<td>47.4%</td>
<td>30.8%</td>
<td>18.2%</td>
<td>302</td>
</tr>
<tr>
<td></td>
<td>Periphery</td>
<td>1.6%</td>
<td>51.2%</td>
<td>28.7%</td>
<td>18.5%</td>
<td>254</td>
</tr>
</tbody>
</table>

Table 6.12: Forest Strata Profiles of Several Postures for *C. campbelli lowei*. 
Figure 6.7: Vertical Distribution of Several Postures for *C. campbelli lowei*.

In both groups, *Clings* were observed most often in the understory (≤5m). Compared to Central Guenons, a larger proportion of Periphery Guenon *Sit* postures occurred in the understory (≤5m) and the upper canopy (20m+), but the percentage difference between groups was minimal (<3%). In the disturbed southern forest, a larger proportion of Periphery Guenon *Stand* postures occurred in the understory (≤5m) and a smaller proportion in the lower canopy (10m–15m) compared to Central Guenons. The vertical distribution of *Recline* postures differed most dramatically between guenon groups. Periphery Guenons engaged in *Recline* postures in both the understory (≤5m) and the lower canopy (10m–15m) 10% less frequently than did Central Guenons and engaged in *Recline* postures nearly 20% more frequently than did Central Guenons in the upper canopy (20m+). Since overall differences in the frequency of *Sit* and *Stand* postures between the postural profiles of each guenon group were greater than differences in *Recline* and *Cling*.
postures, and collectively *Sit* and *Stand* postures accounted for more than 95% of all Rest postures, these postures likely drove intraspecific postural variation for guenons.

Periphery guenons engaged in *Stand* postures during Rest more frequently than did Central Guenons. Since *Stand* postures occurred in the forest understory at a higher frequency for Periphery Guenons than for Central Guenons, I argue that differences in the nature of the understory in the two forest types may explain intraspecific differences in the use of *Stand* postures. Many have argued that the ability to grasp and balance on thin branches has significantly influenced aspects of primate biomechanics, contributing to primate anatomical differentiation both within the Primate Order and away from other mammalian clades (Cartmill, 1972; Sussman, 1991; Larson et al., 2000; Schmitt, 2003). Whereas colobus typically propped themselves above or along the side of tall vine heaps in disturbed southern forest understory, guenons tended to be found within these masses of vegetation. The interior of this clumped understory vegetation featured thin, flexible supports woven loosely together in a complex labyrinth of vertical, horizontal and oblique supports.

The smaller body size of guenon females probably facilitated movement within this maze of supports. However, the size and flexibility of thin supports that characterized understory vine heaps may have also limited the full range of guenon postural behavior. Though supports of all sizes and orientations could be found in each forest stratum, long, large horizontal and oblique supports (i.e., Boughs and
larger Branches) were probably most rare among the saplings, trunks, and flexible vegetation in the forest understory (McGraw, 1996a). Primates can balance their body mass above supports too thin to singularly bear their weight by distributing their mass across multiple supports (Fontaine, 1990). When larger supports were unavailable, guenon females would often distribute their weight across multiple supports (Figure 6.8). Stand postures allowed female guenons to grasp potentially four separate supports which could have increased stability amid particularly small, flexible Twigs found in dense southern forest understory (Larson et al., 2000). Therefore, the fact that Periphery Guenons used the lowest arboreal stratum (≤5m) slightly more often (~3%) than did Central Guenons may explain the increased frequencies of Stand observed there.

Figure 6.8: Stand Postures in Forest Understory. Thin supports of differing orientations were ubiquitous in the forest understory, particularly in disturbed southern forest. When single supports capable of bearing a guenon’s weight were unavailable, monkeys often distributed their body mass across several different supports.
It is possible that guenon foraging strategies also encouraged the more frequent adoption of Stand postures in southern forest. Guenons are a mostly frugivorous clade of monkeys that supplement their fruit-based diet with animal prey and occasionally leaves (Cords, 1984; Gautier-Hion, 1988). Buzzard (2006) found that *C. campbelli lowei*’s close phylogenetic relative *C. campbelli campbelli* in the Ivory Coast’s Tai Forest depended primarily on fruit (46%) and secondarily on animal prey (33%) during most of the year. Buzzard (2006) also noted that *C. campbelli campbelli* fed on animal matter more than twice as often as either of the other two guenon species he studied and consumption of animal matter exceeded consumption of fruit during periods of the year that fruit was less available. At BFMS, I did not collect specific dietary data (see Chapter 2) but insects and insect larva were regularly consumed by both Periphery Guenons and Central Guenons. While traveling, guenons in both forests would flip over leaves, pull prey out of spider webs, and frequently scan the foliage for potential food resources. During these foraging bouts, guenons would typically come to a brief Rest, engage in a Stand posture while scanning surrounding leaves or branches for food or alternate locomotor routes, and then continue their travel (Figure 6.9). This may be a characteristic guenon foraging strategy as McGraw (1998b) noted a very similar foraging pattern for *C. campbelli campbelli* in the Tai Forest, Cote d’Ivoire.
Figure 6.9: Guenon Foraging Postures. These photos show a male (left) and a female (right) guenon scanning the leaves of higher branches. This was a common strategy for identifying potential food resources for all guenons.

The increased patchiness and competition associated with insectivory (Oates, 1987) may have encouraged female guenons in southern forest to more frequently adopt postures that enhanced their ability to acquire insect prey. As forests become fragmented, the increasing number of forest edges exposes a greater proportion of the forest floor to sunlight, often stimulating plant growth (Murcia, 1995). Fragmentation has resulted in both increases and decreases in insect herbivory, a sign of insect abundance, and by association increases and decreases in insect predation (Ruiz-Guerra, 2010). In southern forest, the dense vegetative masses in the forest understory are a product, at least in part, of past anthropogenic disturbance and fragmentation. If past forest clearing reduced upper canopy food abundance (i.e., fewer fruiting trees) or increased the challenge of acquiring food in southern forest canopy (i.e., fruit/insects more patchily distributed), it is possible that Periphery Guenons might have sought alternative food sources. Buzzard (2006)
found that *C. campbelli campbelli*, *C. campbelli lowei*’s sister clade, increased rates of insectivory when fruit became less available. Vine tangles are reportedly rich in insect biomass and a frequent feeding location for highly insectivorous primates (Youlatos, 1999). In southern forest, the dense entangled vines that dominated the southern forest understory likely offered a wealth of insect resources for Periphery Guenons. The same densely tangled vegetation might also have impeded the Periphery Guenons’ range of vision. The exterior surface of dense heaping vine tangles in southern forest were composed of tightly woven vines, leaves, and branches into which, and presumably out of which, was quite difficult to see. This may have made insect/fruit resources challenging to identify in southern forest understory.

Potentially increased insectivory and increased feeding competition associated with more difficult to identify and acquire competitive food resources in southern forest could have contributed to the increased frequency of guenon *Stand* postures in southern forest. *Stand* postures can be viewed as a transitional state between locomotor behaviors (Rose, 1974) and place an animal in a position from which they can quickly run, climb, or leap to acquire potential prey items (McGraw, 1998b). I suggest that Periphery Guenons may have used *Stand* postures at higher frequency and consequently *Sit* postures at a lower frequency than did Central Guenons for three reasons: 1) they used the understory more often than did Central Guenons; 2) *Stand* postures allowed them to distribute their body mass across multiple flexible supports found commonly in disturbed southern forest understory;
and 3) *Stand* postures facilitated rapid transitioning into different locomotor modes needed to quickly acquire competitive food resources in the tangled vegetation dominating southern forest understory.

In summary, I argue that intraspecific postural differences between colobus and guenon groups in two forest types at BFMS can be explained by contrasting patterns of habitat use. Both species used lower forest strata more often in highly disturbed southern forest than in less disturbed western forest. Lower strata may have provided routes between feeding and resting locations within each monkey species’ home range for which direct upper canopy alternatives were not available. Additionally, lower strata may have contained alternate and/or supplementary food resources. Regardless of why each species were drawn to the lower canopy and/or understory, the increased use of certain postures in southern forest is likely a product of the architectural properties of these strata. For colobus, I argue that the intermediate and lowest arboreal forest strata in southern forest contained many flexible supports on which maintaining *Recline* postures was challenging. For guenons, the architectural properties and density of tangled vegetation in southern forest understory likely limited visibility and may have made finding food resources more challenging. As highly competitive feeders, guenons may have adopted *Stand* postures to better support their weight on flexible, thin supports found in dense understory and to rapidly transition between locomotor modes in search of elusive prey.
The question remains, though, do these intraspecific postural differences pose a challenge to our understanding of broad form-function associations in non-human primates? I argue that intraspecific differences in postural profiles identified in this study do not contradict previous findings that primate positional behavior is an inherently conservative phenomenon (e.g., Doran and Hunt, 1994; Garber and Pruetz, 1995; McGraw, 1996b). Researchers highlighting the consistency of primate positional behavior are, in effect, affirming the constraints that an animal's morphology, physiology, and phylogeny place upon the full range of a primate's postural and locomotor behaviors. In this study, those same constraints are clear. Both monkey species in more disturbed southern forest adopted postures at different frequencies than conspecifics in less disturbed western forest, but these differences might best be described as variations in a similar overall pattern. In other words, when postures are ranked from most used to least used, each species’ postural preferences remained consistent across both forest types (Table 6.13). Sit was the dominant posture utilized by females in every study group. The second most frequently used posture for both colobus groups was Recline while for both guenon groups it was Stand followed by Recline. Despite substantial differences in forest architecture and support usage, neither species in disturbed forest exhibited substantially altered ranked postural preferences (e.g., guenons in disturbed forest standing more than sitting). Nor did either species adopt novel postures (e.g., guenons suspending from their hindlimbs) to negotiate the unique architectural properties of southern forest. This suggests that something intrinsic to these animals
(e.g., morphology, body mass, dietary preferences) constrains the types of postures they are likely to exhibit irrespective of the type of environment in which they find themselves.

<table>
<thead>
<tr>
<th>Postures Ranked by Overall Frequency (From Most Common to Least Common)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Colobus</strong></td>
</tr>
<tr>
<td>1. <em>Sit</em></td>
</tr>
<tr>
<td>2. <em>Recline</em></td>
</tr>
<tr>
<td>3. <em>Other</em></td>
</tr>
<tr>
<td>4. <em>Cling</em></td>
</tr>
<tr>
<td>5. <em>Other</em></td>
</tr>
</tbody>
</table>

**Table 6.13: Postures Ranked by Overall Frequency.** This table lists for each species the ranked sequence of postures used from those most frequently used to those least frequently used.

**Summary**

I tested whether groups of *C. vellerosus* and *C. campbelli lowei* inhabiting areas of forest at BFMS characterized by differing levels of anthropogenic disturbance vary their postural behavior in response to differences in forest structure and support use. Using data collected through instantaneous focal sampling, I compared pooled postural profiles for females from each of these forest types for both species. Row x Column tests for intraspecific differences in overall postural profiles as well as postural profiles during maintenance activities revealed some significant differences. The results of these tests are outlined below:

1. Both species exhibited intraspecific variation between forest types in their overall postural profiles.
2. Postures adopted during the Rest activity accounted for the vast majority of all postures observed for both species and likely drove overall intraspecific differences in postural profiles.

3. I posit that for colobus in disturbed southern forest, the understory and lower canopy may have provided more direct pathways between locations within their respective home ranges when direct upper canopy routes were not available. While resting in these lower forest strata, colobus in southern forest likely encountered numerous thin, flexible supports upon which Recline postures were not possible. This may account for increased frequencies of Sit and decreased frequencies of Recline for colobus in southern forest.

4. Guenons in more disturbed southern forest exhibited a higher frequency of Stand and a lower frequency of Sit postures than those in western forest. I argue that Stand postures may be more frequent in southern forests because this posture allowed guenons to distribute their weight across numerous flexible supports within the web of interwoven vegetation characterizing the understory. Further, Stand postures provide easy transitions into locomotor behaviors and facilitate rapid acquisition of fruit and insect resources. The disturbed upper canopy may have forced guenons in southern forest to look
to the understory for alternate food resources though future dietary study is needed to confirm this.

5. When postures are ranked from most common to least common, colobus and guenons in both forests maintained the exact same sequence of preferred postures. This suggests that while postures significantly varied between forest types, this variation is still largely constrained by an animal’s evolutionary history.

Intraspecific differences in posture identified in this study suggest that primates do adjust their patterns of positional behavior under conditions of habitat disturbance. For monkey species at BFMS, I argue that this postural variation stems from the combined interaction of dietary patterns, morphological constraints, and habitat use. Intraspecific differences in postural profiles between forests offer insight into how each species responds behaviorally to increasingly disturbed habitat. Nevertheless, this postural variation appears to be limited to subtle changes in the frequency that certain postures are used rather than dramatic changes in the overall preference for different postures. In chapter 6, I compare locomotor profiles for females of both monkey species to see if the trends identified for postures (i.e., similar profiles with statistically significant variations in the frequencies of certain behaviors) holds true for social and non-social locomotion.
Chapter 7: Intraspecific Differences in Locomotion

Introduction

Locomotion comprises the non-postural component of Prost’s (1965) classic positional behavior gradient. For Prost (1965), locomotion included behaviors in which shifts in body mass exceeded some theoretical and largely undefined threshold. In practice, researchers of primate positional behavior have defined locomotor activities as those behaviors that are used to move an animal between physical locations and can include climbing, quadrupedal locomotion, arm swinging, leaping, and a variety of other travel-associated activities (e.g., Morbeck, 1977; Fleagle, 1980; Fontaine, 1990; Garber, 1991; McGraw, 1996b; Johnson and Shapiro, 1998; Thorpe and Crompton, 2006).

Cant (1992) described primate locomotor decisions as strategies aimed at shortening travel paths between range locales and accessing resources in as competitive a manner as possible. According to the author, these decisions are based on solving four problems: finding direct paths, efficiently using large vertical supports, crossing canopy gaps and moving quickly across chosen arboreal pathways. Of all these challenges, many researchers have stressed the significant role that crossing canopy gaps play in shaping primate locomotor strategies (e.g., Fleagle, 1985; Cant, 1992; Cannon and Leighton, 1994; McGraw 1998a). For
example, Cant (1992) called the manner that primates cross gaps “probably the single most important determinant of path length” (p. 280). In other words, as arboreal primates select travel routes between locations in their home range, the presence or absence of gaps they encounter and the costs incurred in crossing those gaps (e.g., risk of falling, energy expenditure) may, in large part, predict the path they choose to take (Cannon and Leighton, 1994).

Due to the suggested importance that gaps play in locomotor decisions, Cannon and Leighton (1994) proposed a model called the Perceived Continuity Index (PCI) to predict the likelihood that an animal will use a particular forest stratum. This model predicts the likelihood of forest strata use based on the frequency of canopy gaps per unit distance (i.e., number of gaps within an average 20 segment of the forest strata), the percentage of gaps narrow enough to be crossed by a species and the median length of continuous canopy structure within a forest stratum. According to this model, those strata with higher PCI values will be perceived as more connected by an animal and therefore more likely to be used. If, as this model predicts, primates use forest strata to differing degrees during periods of travel based on the nature of support architecture within each stratum, then it is possible that architectural differences between forest strata may influence other aspects of locomotion as well.

Forests are dynamic environments and forest architecture tends to exhibit both vertical and horizontal heterogeneity (Fleagle, 1985; Cannon and Leighton, 1994). This heterogeneity might be exacerbated in forests experiencing internal
fragmentation due to anthropogenic disturbance (Marsh, 2003). Even in intact forests, arboreal primates might be expected to regularly encounter breaks between tree crowns and/or between supports separated by great distances in all forest strata (McGraw, 1998a). In other words, primates will face gaps that need to be crossed or avoided by taking alternate routes. Fleagle (1985) argued that variation in primate body size is associated with the tendencies for different primate species to exhibit different frequencies of locomotor behaviors (i.e. bridging, climbing, suspensory locomotion, and leaping). Large-bodied primates, he argued, might exhibit higher frequencies of bridging/climbing because their longer reach allows them to cross more gaps than a smaller primate in the same environment. Because arboreal food resources are often located on thin supports, primates frequently forage within small-branch environments (Cant, 1992). However, large body mass will also limit that locomotion to those supports that can bear their weight. Fleagle (1985) suggested that this may explain why larger-bodied primates often possess suspensory morphologies that facilitate below-branch locomotor behaviors. If small-bodied primates without such suspensory adaptations choose to cross the same gaps as those crossed by larger primates, leaping may be the only realistic locomotor option.

Travel patterns are dependent not only on forest architecture but also on the anatomy of the primates inhabiting that forest. This becomes apparent when one compares two morphologically divergent monkey clades: colobines and cercopithecines. Neither of these clades possesses the suspensory adaptations of
platyrhines or hominoids (Napier and Napier, 1967) and they rarely exhibit suspensory locomotion (Morbeck, 1977; McGraw 1998a). Those animals that cannot rely on suspensory locomotion to facilitate crossing main canopy gaps may instead choose to cross those gaps through leaping (Cannon and Leighton, 1994). For colobines, adaptations of the lower limb enable them to perform extended leaps (e.g., long hindlimbs: Strasser, 1992; Oates and Davies, 1994). When crossing between tree crowns in the main canopy, McGraw (1998a) suggested that some colobus species may initiate leaps inward from flexible supports found along the periphery of those crowns. This effectively increases the distance each leap needs to cover but provides a more stable support from which to initiate leaps.

Without the leaping specializations possessed by colobines, cercopithecines approach canopy gaps differently. Cannon and Leighton (1994) argued that long-tailed macaques (*Macaca fascicularis*) frequently encountered gaps they could not bridge (>50% of gaps in all five forest strata recognized in the study). When they chose to cross those gaps through leaping, long-tailed macaques tried to minimize those gaps by leaping from the extreme periphery of tree crowns. The authors suggested that leaping from this part of the tree crown was costly for two reasons: 1) the flexible branches along the periphery of tree crowns were unstable and thus increased the risk of misjudging a leap or collapsing supports; 2) as macaques moved further out on flexible supports, these supports deformed under their body mass, effectively increasing the size of those gaps and energetic costs needed to cross them. Cannon and Leighton (1994) argued that when long-tailed macaques
judged the majority of gaps too risky or energetically costly to cross in a forest stratum, they would instead select alternate routes and strata that could be traversed using more preferred locomotor behaviors. This explains why, for instance, the authors recorded a high frequency of quadrupedal locomotion (59.8%) during travel compared to a low frequency of leaping (6.4%) or bridging (0.9%).

The different locomotor strategies exhibited by macaques and colobus in the previous examples illustrate the complexity of primate locomotor decisions. Napier (1967) stated that “in order to understand the adaptive significance of the locomotion of living primates and of the part locomotion has played in the dispersal and taxonomic differentiation of the Order, reference must be made to the evolutionary history of the group particularly in the context of past ecology” (p. 333). Napier (1967) rightly argued that locomotion is influenced not just by the present ecological conditions in which an animal finds itself (e.g., the location of food items, the presence of canopy gaps) but also the evolutionary history that molded the anatomy and physiology of that animal. In this chapter, I test whether differences in forest architecture between two forest types at BFMS are sufficient to produce significant intraspecific variation in *C. vellerosus* and *C. campbelli lowei* locomotor profiles. Significant intraspecific variation in locomotor profiles will be examined in the context of architectural differences between forest types as well as the morphology and dietary tendencies of the two study species.
Hypotheses

- Research Question: Do the overall locomotor profiles of colobus and guenons living in more interconnected western forest at BFMS differ from the locomotor profiles of the same species living in more disturbed southern forest?

I test each of the following hypotheses regarding intraspecific locomotor variation summarized in Table 7.1. I offer justifications for these hypotheses below and make predictions regarding how the frequencies of specific locomotor behaviors might be altered in more disturbed southern forest.

<table>
<thead>
<tr>
<th>Predictions</th>
<th>Intraspecific Locomotor Differences</th>
<th>Predicted Cause of Change</th>
<th>Type of Change in More Disturbed Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₀</td>
<td>No change for either species</td>
<td>Morphological constraints</td>
<td>No change; statistically similar locomotor profiles</td>
</tr>
<tr>
<td>H₁</td>
<td>Both species change</td>
<td>Less interconnected upper canopy</td>
<td>Reduced frequency of Quadrupedalism; increased frequency of gap-associated locomotor behavior</td>
</tr>
</tbody>
</table>
| H₂          | Change in guenons but not colobus | Feeding competition       | - Colobus: No change  
- Guenons: Increased frequency of Horizontal Climb and Leap |
| H₃          | Both Species Change               | Body size differences     | - Colobus: Increased frequencies of Bridge and/or Horizontal Climb  
- Guenons: Increased frequency of Leap |

Table 7.1: Predictions for Intraspecific Locomotor Differences.

H₀ predicts that the locomotor profiles of both species will not differ significantly between less disturbed western forest and more disturbed southern forest.
forest despite differences in forest structure and the use of supports/forest strata. This prediction is based on results of previous studies that have found both locomotor and postural profiles to be conservative across different forest habitats (e.g., Doran and Hunt, 1994; Garber and Pruett, 1995; McGraw 1998a). These studies suggest that primate species, as a result of their evolutionary history, are constrained to a certain range of locomotor behaviors. This hypothesis predicts that all forest at BFMS contains numerous canopy gaps and that colobus and guenons crossing those gaps will choose to do so using the same locomotor strategies.

H₁ predicts that both species will significantly alter their locomotor profiles in disturbed southern forest and that these alterations will correspond to differences in forest architecture. Cant (1992) argued that primates competing over food should strive to move in as short a path as possible between feeding locations. Under this hypothesis, both monkey species in southern forest are predicted to have minimized travel time between distant points in their range. By shortening pathways and moving directly between feeding locations, primates will increase their likelihood of acquiring food resources before their competitors (Cant, 1992). In chapter 5, I showed that both colobus and guenons in southern forest used lower supports at higher frequencies than they did in less disturbed western forest. Due to the presumed high proportion of thin supports in these strata (McGraw, 1996a), the selective use of supports large enough to facilitate Quadrupedalism may produce too circuitous of travel pathways and, in some cases, large supports may simply be unavailable. Therefore, H₁ predicts that southern forest monkeys will engage in
higher frequencies of gap-crossing locomotor behaviors (e.g., *Leaps, Horizontal Climb, Bridge*) than conspecifics in less disturbed western forest.

*C. vellerosus* and *C. campbelli lowei* possess very different dietary strategies. *C. vellerosus* at BFMS are highly folivorous primates that feed on the foliage of numerous tree species spread across their home range (Saj et al., 2005; Saj and Sicotte, 2007a). Oates (1987) argued that folivorous primates should experience less intragroup feeding competition than do more frugivorous or insectivorous primates due to the fact that leaves are less patchily distributed. If feeding competition is low between folivorous colobus throughout BFMS, H2 predicts that they will be under minimal pressure to alter locomotor profiles in disturbed forest. Therefore, Redtail Colobus in southern forest will maintain locomotor profiles that are statistically identical to those of Wawa Colobus in western forest. If we assume similarity in diet between *C. campbelli lowei* and other closely related guenons (Gautier-Hion, 1988; Buzzard, 2006), guenons at BFMS feed most frequently on fruits and rely more on insects as fruits become unavailable. If feeding competition is high in guenons, H2 predicts that they will be more inclined than colobus to shorten pathways between feeding sites. Guenons are known to be highly competitive feeders, especially when population densities are high (Gautier-Hion, 1988). If feeding competition drove guenon locomotion at BFMS, they are predicted to use whatever locomotor strategies move them quickly between feeding sites. In western forest, Central Guenons might have been able to use the more intact canopy to efficiently move through *Quadrupedalism*. With fewer direct arboreal pathways
on which to move via Quadrupedalism, Periphery Guenons are predicted to exhibit higher frequencies of Horizontal Climb and Leap, both locomotor behaviors that might move them directly between feeding sites in vine-tangled, southern forest understory.

H₃ predicts that body size differences between C. campbelli lowei and C. vellerosus will drive intraspecific variation in locomotor profiles between forest types at BFMS. Fleagle (1985) predicted that smaller primates will encounter more gaps that they can cross only through leaping than will larger primates in the same forest. When alternative routes including large supports that facilitate Quadrupedalism are unavailable or too indirect, canopy gaps along more direct arboreal pathways might be crossed differently by the two monkey species. If these gaps are more frequently encountered by both species in southern forest, H₃ predicts that smaller-bodied Periphery Guenons in southern forest will engage in Leap more frequently than do guenons in western forest. In contrast, larger-bodied Redtail Colobus in southern forest will engage in Bridge and Horizontal Climb more frequently than do colobus in western forests.

**Methods**

I collected data on the locomotion of two primate species at BFMS via a three-minute instantaneous focal sampling technique. The sampling methods are described in detail in Chapter 4. The forest characteristics for each study groups’ home ranges are described in Chapter 3.
At each time point, I recorded the following data:

- Sex
- Support Characteristics: Size and Orientation
- Forest Stratum
- Maintenance Activity
- Postural or Locomotor Behavior

To avoid any confounding affect that sex differences might have had on these intraspecific comparisons, I included only data collected from adult females. Sex differences in locomotion will be examined in Chapter 8.

When I recorded a locomotor behavior, I classified this behavior into one of two locomotor-associated maintenance activities. These activities are listed and defined in Table 7.2. Social Locomotion included locomotor behaviors that occurred in conjunction with a social activity (e.g., fighting, displaying, fleeing). All other locomotor behaviors were categorized as Non-Social Locomotion. This distinction is important because the factors governing these two types of movement may differ greatly. Non-Social Locomotion included movement associated with particular forest locations (e.g., movement toward a feeding site, resting trees) as well as exploratory movement (i.e., foraging). During Non-Social Locomotion, movements were typically responses to potential threats and therefore were as much influenced by the movements of the individual a focal animal was pursuing or retreating from as by the forest structure upon which that travel occurred. I judged that locomotor
decisions made during Social Locomotion differed enough from those made during Non-Social Locomotion to warrant their separation into separate activities.

Other studies of primate locomotion have further divided the locomotor behaviors I refer to as Non-Social Locomotion into separate travel and foraging activities (e.g., McGraw, 1998a). Differentiating between locomotion associated with foraging and that associated with travel was unreliable at BFMS for a number of reasons. First, poor visibility due to impassible, dense understory made classifying whether a move terminated in a feeding bout challenging. Second, *C. campbelli lowei* fed continuously throughout the day and did not engage in distinct feeding and long-distance travel periods. Even when traveling from one end of their range to the other, individuals would regularly forage throughout the canopy as they moved. For both these reasons, I pooled all Non-Social Locomotion together into a single category for both species.

<table>
<thead>
<tr>
<th>Locomotor Maintenance Activities</th>
<th>Definition</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Social Locomotion</td>
<td>Movement of the body unassociated with social activities</td>
<td>- Long-distance travel across range - Short-distance travel between feeding sites</td>
</tr>
<tr>
<td>Social Locomotion</td>
<td>Movement of the body associated with dominance displays or other social activities</td>
<td>- Chasing - Leaping displays - Fighting</td>
</tr>
</tbody>
</table>

*Table 7.2: Locomotion-Associated Maintenance Activities.*

Prior to collecting field data, I created an extensive list of locomotor categories to be used in this study. These categories were based loosely on Hunt et
al.’s (1996) standardized list of positional behavior terms and were modified to increase their comparability with previous studies on closely related primate species (e.g., McGraw, 1996a, McGraw, 1998a). Each locomotor category recorded during this study is listed and defined in Table 7.3.

<table>
<thead>
<tr>
<th>Locomotion Class</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arm Swing</td>
<td>Below branch movement with one forelimb gripping a support and locomotion produced through the rotation of the shoulder joint and the momentum of the body weight carried below that support</td>
</tr>
<tr>
<td>Bipedal Hop</td>
<td>Short jumps initiated from a bipedal posture and landing in a bipedal posture</td>
</tr>
<tr>
<td>Bounding</td>
<td>Quadrupedal locomotion along a continuous support characterized by repeated synchronous contacts of both forelimbs with a support followed by synchronous contact of both hindlimbs with a support</td>
</tr>
<tr>
<td>Bridge</td>
<td>Movement across canopy gaps by pulling one’s weight from one side of the gap to the other while maintaining contact between the limbs and supports on either side of the gap</td>
</tr>
<tr>
<td>Drop</td>
<td>Movement from a higher support to a lower support with no clear propulsion provided by either the forelimbs or hindlimbs</td>
</tr>
<tr>
<td>Forelimb Climb</td>
<td>Movement between disconnected but nearby supports involving substantial forelimb propulsion</td>
</tr>
<tr>
<td>Headfirst Descent</td>
<td>Downward movement with the head oriented below the torso on vertical or oblique supports</td>
</tr>
<tr>
<td>Hindlimb Climb</td>
<td>Movement between disconnected but nearby supports involving one or more small leaps propelled by the hindlimbs</td>
</tr>
<tr>
<td>Leap</td>
<td>Long-distance locomotion between widely spaced supports involving substantial hindlimb propulsion</td>
</tr>
<tr>
<td>Mount</td>
<td>Body mass shifts associated with mating for both males and females</td>
</tr>
<tr>
<td>Quadrupedal Run</td>
<td>Fast quadrupedal locomotion along a continuous support in which both forelimbs and both hindlimbs contact supports asynchronously</td>
</tr>
<tr>
<td>Quadrupedal Walk</td>
<td>Slow quadrupedal locomotion along a single support</td>
</tr>
<tr>
<td>Tripedal Run</td>
<td>Fast movement along a continuous support on three limbs; typically carrying an object with the fourth limb</td>
</tr>
<tr>
<td>Tripedal Walk</td>
<td>Slow movement along a continuous support on three limbs; typically carrying an object with the fourth limb</td>
</tr>
<tr>
<td>Vertical Ascent</td>
<td>Upward movement along a vertical or oblique support with head oriented above the torso</td>
</tr>
<tr>
<td>Vertical Descent</td>
<td>Downward movement along a vertical or oblique support with head oriented above the torso</td>
</tr>
</tbody>
</table>

**Table 7.3: Recorded Locomotor Categories.**
I used Row x Column tests for independence to compare frequency tables generated for each group’s overall locomotor profile and each group’s locomotor profile by maintenance activity. Significant results of these tests (p<0.05) indicate a dependent relationship between column and row variables. For example, if forest type and locomotion were used to generate a frequency table for locomotor behaviors, a significant result in a R x C test comparing these profiles indicated that the two locomotor profiles differed more than might be expected by chance. During analysis, data for similar locomotor behaviors were pooled into broad locomotor categories. These pooled categories produced fewer columns on frequency tables and were necessary in order to avoid producing frequency tables in which more than 20% of entries had expected values <5 (minimal requirements for statistical tests—see Chapter 4; Sokal and Rohlf, 1995; McKillup, 2005). In this study, pooling data was appropriate because broad locomotor categories reflected behaviors used to address similar structural challenges and created a dataset comparable to other positional behavior studies (particularly McGraw, 1996a, McGraw, 1998a—see Chapter 9). In Table 7.4, I list each pooled locomotor category, the locomotor behaviors included in each category and a brief rationale for grouping these behaviors. The “Other” category consisted of rare locomotor behaviors (usually <10 observations). Many of the most common pooled locomotor categories are illustrated in Appendix A.
<table>
<thead>
<tr>
<th>Pooled Locomotor Category</th>
<th>Locomotor Modes Included</th>
<th>Structural Challenges</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drop</td>
<td>Drop</td>
<td>Rapid descent between supports of differing heights without propulsion</td>
</tr>
<tr>
<td>Horizontal Climb</td>
<td>Forelimb Climb</td>
<td>Movement between proximate but discontinuous supports</td>
</tr>
<tr>
<td>Leap</td>
<td>Leap</td>
<td>Movement between supports that could not be crossed by bridging, climbing, etc.; Must include an aerial phase</td>
</tr>
<tr>
<td>Vertical Climb</td>
<td>Vertical Ascent</td>
<td>Controlled upward or downward movement along vertical or near-vertical supports</td>
</tr>
<tr>
<td>Quadrupedalism</td>
<td>Bounding</td>
<td>Direct travel along continuous supports</td>
</tr>
<tr>
<td>Other</td>
<td>Armswing</td>
<td>Various structural challenges for locomotor classes that were rarely observed</td>
</tr>
<tr>
<td></td>
<td>Bipedal Hop</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bridge</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mount</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tripedal Walk</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tripedal Run</td>
<td></td>
</tr>
</tbody>
</table>

Table 7.4: Pooled Locomotor Categories. The right column briefly describes the nature of structural challenge that each locomotor category addressed.

Results

C. vellerosus: Intraspecific Comparisons for all Locomotor Behaviors

The frequencies of locomotor behaviors for female Wawa Colobus and Redtail Colobus are listed in Table 7.5 and compared in Figure 7.1. For female colobus in less disturbed western forest (Wawa Colobus) and more disturbed southern forest (Redtail Colobus), forest type and locomotor category proved to be independent of one another (G-test: 2.848; p=0.723). In other words, there was no significant difference in the overall locomotor profile between colobus groups at BFMS inhabiting forests characterized by differing levels of habitat disturbance.
<table>
<thead>
<tr>
<th>Group</th>
<th>Drop</th>
<th>Horizontal Climb</th>
<th>Leap</th>
<th>Quadrupedalism</th>
<th>Vertical Climb</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>1.8%</td>
<td>20.0%</td>
<td>33.3%</td>
<td>33.5%</td>
<td>9.9%</td>
<td>1.5%</td>
<td>669</td>
</tr>
<tr>
<td>Redtail Colobus</td>
<td>3.0%</td>
<td>20.6%</td>
<td>34.5%</td>
<td>30.8%</td>
<td>9.5%</td>
<td>1.6%</td>
<td>608</td>
</tr>
</tbody>
</table>

Table 7.5: Overall Locomotor Profiles for *C. vellerosus*.

![Graph showing locomotor profiles for Wawa Colobus (Less Disturbed Forest) and Redtail Colobus (More Disturbed Forest).]

**Figure 7.1: Comparison of Overall Locomotor Profiles for *C. vellerosus*.

*C. campbelli lowei*: Intraspecific Comparisons for all Locomotor Behaviors

The frequencies of locomotor behaviors for female Central Guenons and female Periphery Guenons are listed in Table 7.6 and compared in Figure 7.2. I identified a dependent relationship between forest type and locomotor behavior (G-test: 15.618; p=0.008). Periphery Guenon females in the more disturbed southern forest engaged in *Quadrupedalism* approximately 6% less frequently than did Central Guenons in unlogged western forest. However, female Periphery Guenons
engaged in *Horizontal Climb* approximately 4% more frequently and *Leap* >2% more frequently. Frequencies of *Vertical Climb* were quite similar between the two guenon groups (approximately 7%). *Drop* and *Other* locomotor behaviors collectively accounted for less than 3% of all locomotor behaviors for each group.

<table>
<thead>
<tr>
<th>Group</th>
<th>Drop</th>
<th>Horizontal Climb</th>
<th>Leap</th>
<th>Quadrupedalism</th>
<th>Vertical Climb</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>1.2%</td>
<td>19.3%</td>
<td>21.1%</td>
<td>49.7%</td>
<td>7.1%</td>
<td>1.6%</td>
<td>1459</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>1.2%</td>
<td>23.4%</td>
<td>23.4%</td>
<td>43.6%</td>
<td>7.6%</td>
<td>0.9%</td>
<td>1293</td>
</tr>
</tbody>
</table>

**Table 7.6: Overall Locomotor Profiles for *C. campbelli lowei*.**

![Graph showing comparison of overall locomotor profiles for Central and Periphery Guenons](image)

**Figure 7.2: Comparison of Overall Locomotor Profiles for *C. campbelli lowei*.**
Locomotor Behaviors by Maintenance Activity: C. vellerosus and C. campbelli lowei

For both species, Non-Social Locomotion was far more common than Social Locomotion. Of the 1277 locomotor behaviors I observed for females of both colobus groups, only 19 occurred during Social Locomotion. Of the 2752 locomotor behaviors I observed for females of both guenon groups, only 174 occurred during Social Locomotion. Because of the low number of observations falling into Social Locomotion, intraspecific comparisons of locomotor profiles for this activity were not considered. When Social Locomotion behaviors are removed from the total pool of locomotor behaviors, the results are unsurprisingly similar to overall locomotor comparisons. Forest type and locomotor behaviors were dependent only for C. campbelli lowei (G-test: 15.640; p=0.008). Forest type and locomotor behaviors remained independent for colobus (Fisher Exact Test: 3.062; p=0.693). Female guenon locomotor profiles during Non-Social Locomotion are considered below.

C. campbelli lowei: Intraspecific Differences during Non-Social Locomotion

The locomotor profiles of female Central Guenons and female Periphery Guenons are listed in Table 7.7 and compared in Figure 7.3. The differences between guenon groups during Non-Social Locomotion are nearly identical to overall locomotor differences between the groups. During Non-Social Locomotion, Periphery Guenons in more disturbed southern forest exhibited lower frequencies of Quadrupedalism (difference of ~6%) and higher frequencies of Leap (difference of ~2%) and Horizontal Climb (difference of ~4%) than did female Central Guenons.
### Table 7.7: Locomotor Profiles for *C. campbelli lowei* during Non-Social Locomotion.

<table>
<thead>
<tr>
<th>Group</th>
<th>Drop</th>
<th>Horizontal Climb</th>
<th>Leap</th>
<th>Quadrupedalism</th>
<th>Vertical Climb</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Guenons</td>
<td>1.3%</td>
<td>19.6%</td>
<td>20.9%</td>
<td>49.6%</td>
<td>7.1%</td>
<td>1.6%</td>
<td>1440</td>
</tr>
<tr>
<td>Periphery Guenons</td>
<td>1.1%</td>
<td>23.9%</td>
<td>22.7%</td>
<td>43.8%</td>
<td>7.7%</td>
<td>0.8%</td>
<td>1266</td>
</tr>
</tbody>
</table>

**Discussion**

In previous chapters, I identified significant intraspecific differences in postural profiles of female colobus and guenons inhabiting different forest types at BFMS as well as differences in the characteristics (size and shape) and vertical distribution of supports used by those females. The fact that locomotor profiles significantly differed between groups of *C. campbelli lowei* but not between *C.
vellerosus is therefore somewhat surprising. What might be driving this inconsistency between species?

In this chapter, I predicted that if females in the Central Guenon and Periphery Guenon groups differed in locomotor profiles then these differences might stem from more frequent use of the forest understory in southern forest. Female guenons in both forest types used the lowest arboreal stratum (≤5m) in the majority (>50%) of observations, but Periphery Guenons in more disturbed southern forest used understory supports (≤5m) approximately 3% more frequently than Central Guenons (chapter 5). Though Periphery Guenons spent a larger proportion of their time in forest understory in southern forest than did Central Guenons in western forest, one cannot assume that the understory was where the majority of guenon locomotion occurred. For example, Periphery Guenons traveled along upper canopy pathways in primary tree corridors at least once a day (Figure 7.4). If guenons regularly traveled in the upper canopy and rested in the forest understory, differences between these forest strata would be important in explaining locomotor profiles. Knowledge of the vertical distribution of locomotor activities may offer a fuller understanding of guenon locomotor strategies. Table 7.8 and Figure 7.5 compare the frequencies at which specific locomotor behaviors occurred in different forest strata.
Figure 7.4: Regularly Traversed Canopy Gap by Southern Forest Guenons.

<table>
<thead>
<tr>
<th>Locomotor Behavior</th>
<th>Group</th>
<th>Stratum I: Ground</th>
<th>Stratum II: ≤5m</th>
<th>Stratum III: 10m–15m</th>
<th>Stratum IV: 20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drop</td>
<td>Central Guenons</td>
<td>0%</td>
<td>27.8%</td>
<td>33.3%</td>
<td>38.9%</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Periphery Guenons</td>
<td>0%</td>
<td>28.6%</td>
<td>35.7%</td>
<td>35.7%</td>
<td>14</td>
</tr>
<tr>
<td>Horizontal Climb</td>
<td>Central Guenons</td>
<td>0%</td>
<td>47.9%</td>
<td>23.0%</td>
<td>29.1%</td>
<td>282</td>
</tr>
<tr>
<td></td>
<td>Periphery Guenons</td>
<td>0%</td>
<td>66.2%</td>
<td>22.5%</td>
<td>11.3%</td>
<td>302</td>
</tr>
<tr>
<td>Leap</td>
<td>Central Guenons</td>
<td>1.7%</td>
<td>42.5%</td>
<td>27.6%</td>
<td>28.2%</td>
<td>301</td>
</tr>
<tr>
<td></td>
<td>Periphery Guenons</td>
<td>3.1%</td>
<td>53.1%</td>
<td>25.7%</td>
<td>18.1%</td>
<td>288</td>
</tr>
<tr>
<td>Quadrupedalism</td>
<td>Central Guenons</td>
<td>7.3%</td>
<td>30.4%</td>
<td>28.7%</td>
<td>33.6%</td>
<td>714</td>
</tr>
<tr>
<td></td>
<td>Periphery Guenons</td>
<td>8.6%</td>
<td>32.8%</td>
<td>34.5%</td>
<td>24.1%</td>
<td>555</td>
</tr>
<tr>
<td>Vertical Climb</td>
<td>Central Guenons</td>
<td>0%</td>
<td>60.8%</td>
<td>24.5%</td>
<td>14.7%</td>
<td>102</td>
</tr>
<tr>
<td></td>
<td>Periphery Guenons</td>
<td>0%</td>
<td>58.8%</td>
<td>30.9%</td>
<td>10.3%</td>
<td>97</td>
</tr>
</tbody>
</table>

Table 7.8: Forest Strata Profiles of Locomotor Behaviors during Non-Social Locomotion for *C. campbelli lowei.*
Figure 7.5: Comparison of the Vertical Distribution of Locomotor Behaviors during Non-Social Locomotion for *C. campbelli lowei*.

*Quadrupedalism, Leap, and Horizontal Climb* accounted collectively for >90% of all Non-Social Locomotion for each guenon group. For both guenon groups, *Quadrupedalism* occurred within all three arboreal strata. Compared to Central Guenon females, Periphery Guenon females engaged in *Quadrupedalism* approximately 10% less frequently in the upper canopy stratum (20m+) and nearly 6% more frequently in the intermediate stratum (10m–15m). It is surprising that understory (≤5m) *Quadrupedalism* would be so common for both guenon groups (>30% of all instances of *Quadrupedalism*). In disturbed southern forest, small, flexible supports (Twigs) tended to dominate the disturbed understory and large supports (Boughs) were rarely located near the ground. I predicted that *Quadrupedalism* would be less common in southern forest because other locomotor behaviors (i.e., *Horizontal Climb* and *Leap*) might be more useful in navigating the
densely tangled and flexible vegetation found there (Figure 7.6). While this turned out to be true, these data suggest that Periphery Guenons were able to find supports on which *Quadrupedalism* was possible even in the forest understory. All guenon females engaged in *Quadrupedalism* more frequently than any other locomotor behaviors and used Boughs and Branches over 80% of the time (Chapter 5). If we can assume large supports were more patchily distributed in southern forest understory, it is possible that Periphery Guenons were at least sometimes selecting supports that facilitated their preferred locomotor behaviors (McGraw, 1998a) rather than those supports that offered the most direct travel routes.

![Southern Forest Understory](image.png)

**Figure 7.6: Southern Forest Understory.** Large arboreal supports (Boughs) were rare in this forest strata. Medium supports (Branches) were more common than large supports but thin, flexible supports (Twigs) and vines dominated the understory.
Though guenons may prefer *Quadrupedalism* over other locomotor behaviors, *Leap* and *Horizontal Climb* frequencies accounted for more than 40% of all Non-Social Locomotion. This is because preferred supports (i.e., those that facilitate or allow for the adoption of preferred above-branch *Quadrupedalism*) are unlikely to be present everywhere a guenon chooses to travel. When those supports are not available, we might expect guenons to resort to alternative locomotor behaviors. Leaping and climbing have inconsistently been associated with movement in the forest understory (Leap: Fleagle and Mittermeier, 1980, Youlatos, 1999; Climbing: McGraw, 1998a). Frequencies of *Leap* and *Horizontal Climb* for Periphery Guenons exceeded corresponding frequencies for Central Guenons only in the forest understory (≤5m). The nature of understory architecture in southern forest may therefore help to explain this difference.

Guenons, like other primates, possess numerous adaptations such as flexible joints and grasping, clawless hands that facilitate movement through the small-branch niche (Rose, 1973; Larson et al, 2000; Schmitt, 2003). In southern forest understory, the guenon's small body size and grasping ability might have facilitated movement between the densely tangled, thin supports found there. When *Quadrupedalism* was not possible (i.e., supports were too thin to support body weight) or inefficient (i.e., pathways with large enough supports to allow *Quadrupedalism* were too indirect), *Horizontal Climb* allowed guenons to move directly toward desired food items by grasping and pulling themselves through this network of criss-crossing supports (Figure 7.7). Periphery Guenons likely engaged
in *Horizontal Climb* more frequently than did Central Guenons because this locomotor behavior offered them perhaps the best and sometime the only way to directly move within this massed vegetation.

![Guenon Climbing in Densely Interwoven Vine Tangles](image)

**Figure 7.7: Guenon Climbing in Densely Interwoven Vine Tangles.** *Horizontal Climb* behaviors facilitated movement inside these dense masses of vegetation.

Though *Horizontal Climb* facilitated movement within the dense vegetation in the southern forest understory, a larger proportion of *Leaps* for Periphery Guenons than for Central Guenons occurred in this stratum. For species in less disturbed primary forest understory, leaping may have offered certain advantages over other locomotor behaviors. For example, Fleagle and Mittermeier (1980) found that among seven platyrrhine species in Surinam, rates of leaping were highest for those species frequenting the forest understory. Several studies have noted an increased
rate of leaping in the forest understory and tied that increase to the high quantity of vertical supports found there (Fleagle and Mittermeier, 1980; Youlatos, 1999). In southern forest at BFMS, however, the nature of the understory is very different. Rather than a series of vertical supports separated by open spaces, southern forest understory appears to be composed of a nearly continuous layer of dense vegetation.

I argue that the homogeneity of southern forest understory is deceptive. The dense understory vegetation clumps around young saplings, surrounds tree trunks and tangles around itself. The result is an understory characterized by an undulating canopy-like layer of vegetation (Figure 7.8). In some areas, this understory “canopy” reached in excess of 5m in height and covered a dense thicket of flexible branches, vines, and twigs. In others, the understory might consist only of 1m or less of tangled vines. Coupled with anthropogenic disturbance in the form of cleared trails, heterogeneity in the southern forest understory created numerous gaps. By comparing several Old World monkey species in the Tai Forest, McGraw (1998a) showed that leaping behavior was associated less with a forest stratum per se and more with the abundance of gaps within that stratum. As a result, monkeys found in any forest stratum where gaps are too large for them to safely cross by climbing might opt to Leap across those gaps (McGraw, 1998a). The fact that overall Leap frequencies for Periphery and Central Guenon groups differed by only a small percentage (~2%) suggests canopy gaps are common throughout all forest strata and types at BFMS. The high proportion of Leaps occurring in the understory of the
Periphery Guenons' southern forest range suggests that both *Leap* and *Horizontal Climb* are effective locomotor strategies for navigating this disturbed habitat.

**Figure 7.8: Undulating Southern Forest Understory.** Trails and massed heaps of understory vegetation created many potential gaps for guenons and colobus to cross.

If, as I argue, differences in the nature of the understory in southern forest can explain altered Periphery Guenon locomotor profiles (i.e., slightly increased *Leap* and *Horizontal Climb* frequencies and decreased *Quadrupedalism* frequency), why do colobus not also alter their locomotion? Female Redtail Colobus in disturbed southern forest and Wawa Colobus in less disturbed western forest exhibited
statistically identical locomotor profiles. This is surprising since these groups
significantly differed in their use of supports (e.g., Redtail Colobus exhibited higher
frequencies of twig use), in the frequencies at which they were found in different
forest strata (e.g., Redtail Colobus exhibited higher frequencies of understory and
lower canopy support use), and in their postural profiles (e.g., Redtail Colobus sat
more frequently and reclined less frequently). I predicted that colobus might be
more resistant to habitat disturbance than are guenons because their preferred
foods (i.e., leaves) are likely more ubiquitous than the fruit and insect resources fed
on by guenons (Oates, 1984). In other words, is it possible that, despite past forest
disturbance and differences in forest understory, Redtail Colobus could meet their
daily metabolic needs by traveling between feeding sites in much the same way as
Wawa Colobus?

In Table 7.9 and Figure 7.9, I compare the vertical distribution of all Non-
Social Locomotor behaviors exhibited by Redtail Colobus and Wawa Colobus
females. Leap and Quadrupedalism collectively accounted for approximately 65% of
all Non-Social Locomotion for each colobus group. Horizontal Climb was the third
most frequently used locomotor behavior and accounted for slightly more than 20%
of all Non-Social Locomotion for each group. It is interesting that these three
locomotor behaviors, though consistent between groups in overall frequencies were
somewhat more variable in vertical distribution. Both colobus groups Leaped at the
highest frequency in the upper canopy (20m+). However, Redtail Colobus in
disturbed southern forest engaged in Leaps approximately 10% more frequently in
the understory (≤5m) and 10% more frequently in the lower canopy (10m–15m) than did Wawa Colobus. In contrast, Wawa Colobus females engaged in Leaps 20% more frequently in the upper canopy. Quadrupedalism followed a similar pattern with higher frequencies in the two lowest arboreal strata for Redtail Colobus females. Horizontal Climb was nearly twice as frequent in the forest understory for Redtail Colobus than for Wawa Colobus. These data suggest that while colobus locomotor profiles were consistent between forest types, habitat disturbance did nevertheless influence some aspects of colobus locomotion, namely where certain locomotor behaviors were likely to occur.

<table>
<thead>
<tr>
<th>Locomotor Behavior</th>
<th>Colobus Group</th>
<th>Stratum I: Ground</th>
<th>Stratum II: ≤5m</th>
<th>Stratum III: 10m–15m</th>
<th>Stratum IV: 20m+</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drop</td>
<td>Wawa Colobus</td>
<td>0.0%</td>
<td>9.1%</td>
<td>54.5%</td>
<td>36.4%</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Redtail Colobus</td>
<td>0.0%</td>
<td>16.7%</td>
<td>38.9%</td>
<td>44.4%</td>
<td>18</td>
</tr>
<tr>
<td>Leap</td>
<td>Wawa Colobus</td>
<td>1.8%</td>
<td>18.8%</td>
<td>20.9%</td>
<td>58.2%</td>
<td>220</td>
</tr>
<tr>
<td></td>
<td>Redtail Colobus</td>
<td>2.0%</td>
<td>27.8%</td>
<td>32.2%</td>
<td>38.0%</td>
<td>205</td>
</tr>
<tr>
<td>Horizontal Climb</td>
<td>Wawa Colobus</td>
<td>0.0%</td>
<td>26.5%</td>
<td>20.5%</td>
<td>53.0%</td>
<td>132</td>
</tr>
<tr>
<td></td>
<td>Redtail Colobus</td>
<td>0.0%</td>
<td>50.0%</td>
<td>14.5%</td>
<td>35.5%</td>
<td>124</td>
</tr>
<tr>
<td>Quadrupedalism</td>
<td>Wawa Colobus</td>
<td>13.2%</td>
<td>5.5%</td>
<td>21.9%</td>
<td>59.4%</td>
<td>219</td>
</tr>
<tr>
<td></td>
<td>Redtail Colobus</td>
<td>14.5%</td>
<td>11.3%</td>
<td>24.7%</td>
<td>49.5%</td>
<td>186</td>
</tr>
<tr>
<td>Vertical Climb</td>
<td>Wawa Colobus</td>
<td>0.0%</td>
<td>12.1%</td>
<td>40.9%</td>
<td>47.0%</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>Redtail Colobus</td>
<td>0.0%</td>
<td>37.9%</td>
<td>29.3%</td>
<td>32.8%</td>
<td>58</td>
</tr>
</tbody>
</table>

Table 7.9: Forest Strata Profiles for C. vellerosus During Non-Social Locomotion.
Unlike Wawa Colobus females who were found most often in the upper canopy stratum, Redtail Colobus were found in the upper and lower canopy stratum at a relatively similar frequencies (approximately 35% of all observations) and in the forest understory approximately 5% more frequently. If habitat disturbance drove differences in the vertical distribution of locomotor behaviors between colobus groups, then we might assume that Wawa Colobus better reflected general forest strata preferences for the species. I have argued that upper canopy pathways, though more preferred by *C. vellerosus* in general, were less available in the southern forest. Redtail Colobus may have more frequently utilized alternate arboreal pathways available in lower strata for Non-Social Locomotion to shorten travel routes (Cant, 1992) or because they were located near alternate food resources (Siemers, 2000). The reduced availability of large supports in the lower
canopy and understory (McGraw, 1996a) likely forced colobus to use thinner supports more frequently.

Intraspecific differences in the vertical distribution of Horizontal Climb and Leap behaviors for colobus at BFMS probably derive from the greater use of lower strata and thinner supports by Redtail Colobus. Higher frequencies of understory Horizontal Climb and understory/lower canopy Leap for Redtail Colobus probably occurred for much the same reason it did for Periphery Guenons. Elevated rates of climbing associated with thin supports have been reported for other black-and-white colobus (McGraw, 1998a). Horizontal Climb may have offered the only means of moving between nearby supports throughout many areas of dense understory vegetation. Whenever colobus encountered gaps in either the lower canopy or the understory, like guenons, they often chose to Leap across those gaps. For example, it was fairly common for colobus sitting atop or along the sides of tangled masses of vegetation in the forest understory to shift positions by leaping to adjacent vine heaps rather than exerting the energy to climb to the ground or work their way through areas of densely tangled vines and/or branches.

The increased frequency of Quadrupedalism for Redtail Colobus in the understory, however, is more puzzling. It is notable that of all five locomotor behaviors, Quadrupedalism exhibited the most variation between Wawa Colobus and Redtail Colobus (i.e., Quadrupedalism was approximately 3% less frequent for Redtail Colobus). While this was not sufficient to produce statistically significant differences in overall locomotor profiles between colobus groups, it is possible that
differences in the vertical distribution of Quadrupedalism in southern forests reflected not an increased use of Quadrupedalism in the understory but rather a decreased use of Quadrupedalism in the upper canopy. With fewer opportunities to move via Quadrupedalism in the upper canopy, rates of Quadrupedalism in the understory would naturally have comprised a larger proportion of all incidences of Redtail Colobus Quadrupedalism.

When compared to members of their respective species in less disturbed western forest, Redtail Colobus females and Periphery Guenon females share a number of features in common:

- Both groups used non-upper canopy arboreal supports more frequently.
- Both groups used flexible, twig-sized supports more frequently.
- Both groups altered postural profiles in ways that might have facilitated foraging and helped to maintain balance in non-upper canopy strata.
- Both groups used Horizontal Climb at higher frequency in disturbed understory.
- Both groups used Leaps more frequently in the understory and less frequently in the upper canopy.

Considered together, these facts suggest that both colobus and guenons altered aspects of their positional behavior (i.e., guenons: postural and locomotor profiles; colobus: postural profiles and the vertical distribution of locomotor behaviors) and habitat usage (i.e., use of forest strata and supports of differing characteristics) when facing habitat disturbance. Despite these commonalities, colobus locomotor
profiles remained more conservative than did guenon locomotor behavior. What might have driven this reduced behavioral plasticity in *C. vellerosus*?

I argue that body size and morphological differences between *C. vellerosus* and *C. campbelli lowei* can best explain why colobus were more conservative than guenons in their overall locomotor profiles despite inhabiting nearly identical home ranges. Small-bodied primates may have greater flexibility in where they choose to travel in a forest ecosystem than do larger-bodied primates (McGraw, 1998a). Frequent exposure to gaps coupled with a wide range of locomotor strategies to cross those gaps could have produced the locomotor variation observed for smaller-bodied *C. campbelli lowei*. If smaller-bodied primates are more likely to encounter gaps that can only be crossed through leaping than are larger-bodied primates (Fleagle, 1985), then we would have expected guenons more often than colobus to be placed in the position of making locomotor decisions regarding canopy gaps. When faced with a gap, a hypothetical guenon might have opted to invest the energy and to take the risk of leaping across it. On the other hand, it might have decided that these costs were too great and chosen instead to take an alternate route [e.g., like macaques in Cannon and Leighton (1994)]. Additionally, smaller-bodied guenons might have been able to better support and balance their reduced body mass above thin supports than could larger-bodied colobus (Fleagle, 1985). When facing a similar subset of thin supports, guenons might have experienced more opportunities for above-branch locomotion (i.e., *Quadrupedalism*) than colobus would have. Forced to cross more gaps and having access to a wider range of
locomotor behaviors, its unsurprising that guenon locomotor profiles would be more flexible than would colobus profiles.

The constraints imposed by the colobus’s larger body size may also be reinforced by their evolutionary history. A recent fossil discovery from a 9.88-9.74 MY-old stratum of the Nakali Formation in Kenya tentatively attributed to the Microcolobus genera displays a number of early African colobine morphologies associated with increased arboreality (Nakatsukasa et al., 2010). In Africa, morphological trends tied to colobine evolution may have been associated with a foraging strategy focused on acquiring and digesting leaves, thus reducing competition with more dominant, speciose and omnivorous cercopithecine clades (Delson, 1994). This specialization in leaves has resulted in gastrointestinal adaptations (i.e., alkaline-rich, sacculated foregut) allowing for more efficient fermentation of polysaccharide cellulose that dominates plant cell walls (Lambert, 1998). In conjunction with this dietary adaptation, the colobine lineage may have evolved enhanced leaping morphologies to facilitate movement between the periphery of tree crowns where many leaf resources are located (Morbeck, 1977; Oates and Davies, 1994; McGraw, 1998a). Central to this evolutionary trend were changes in relative limb length. Many researchers have noted associations between postcranial morphology and locomotor behavior (e.g., see various authors in Gebo’s (1993) edited volume). For example, primates that leap frequently tend to possess longer hindlimbs (Napier and Napier, 1967). These long hindlimbs may serve the dual function of increasing the distance of any given leap and dissipating the forces
generated when contacting the terminal support (Strasser, 1992). Fleagle (1976) compared the skeletal anatomy of two arboreal langurs species and argued that the lower intermembral index in *P. melalophos* was associated with leaping while the higher index in *P. obscura* was associated with moving the center of body mass nearer to supports to help facilitate balance issues associated with arboreal quadrupedalism.

Without access to skeletal remains, it is difficult to say with certainty how different *C. campbelli lowei* and *C. vellerosus* are in terms of their relative limb lengths; however, intermembral indices for other colobus and guenon species indicate that guenons tend to have a higher Intermembral Index (IMI average of 86) than do colobus (IMI average of 79) (Napier and Napier, 1967; Fleagle, 1999). Comparing primates that differ in limb morphology is challenging as non-linear allometric differences mean that one-to-one comparisons of certain morphological measures (e.g., intermembral index) may be misleading without considering body size (Strasser, 1992). Strasser (1992) showed, however, that colobines tend to possess longer hindlimb longbones than would a cercopithecine of even a comparable body size. These long hindlimbs have been noted as one of the defining postcranial skeletal characteristics that distinguishes the colobine clade from cercopithecines (Oates and Davies, 1994; Fleagle, 1999).

Leaping specializations in *C. vellerosus* may have influenced their locomotor tendencies in a number of ways. Among black-and-white colobus, suspensory locomotion is rare and *Quadrupedalism* and *Leap* are the most common locomotor
strategies (Morbeck, 1977; McGraw, 1996a). Quadrupedalism and Leap were used at roughly similar frequencies by C. vellerosus at BFMS and both to a greater degree than Horizontal Climb. Even when locomoting via Quadrupedalism, C. vellerosus often used a bounding gait that typically consisted of a series of short consecutive Leaps along a single continuous oblique or horizontal support (Figure 7.10). Morbeck (1977) argued that another black-and-white colobus, C. guereza, used Leap behaviors most frequently to move short distances between feeding patches or during social activities. I argue that when ursine colobus encountered even small canopy gaps, they were more likely to Leap than were guenons because their limb morphology facilitated that behavior. While colobus engaged in Horizontal Climb when it was needed, their tendency to fall back on Leaps, whenever possible, could have constrained their locomotor profiles and resulted in a lack of intraspecific variation.
Figure 7.10: Colobus Bounding. Note the forelimbs and hindlimbs strike the ground in unison separated by a distinct aerial phase much like in leaping.

In contrast, arboreal guenons are a diverse clade of morphologically generalized quadrupeds capable of living in a variety of environments and forest strata but exhibiting very few morphological traits that clearly distinguish arboreal from semi-arboreal species (Gebo and Sargis, 1994; Butynski, 2002). Fossil guenons are the product of a period of monkey diversification following the Late Miocene with the earliest definitive guenon fossils appearing in the Plio-Pleistocene (~3mya) (Leakey, 1988). The morphological generalization that characterizes the modern guenon clade is probably rooted in a semi-terrestrial, forest-dwelling, largely frugivorous ancestry and has persisted since members of clade emerged in the fossil record (Leakey, 1988).
C. campbelli lowei at BFMS clearly preferred the forest understory. In this forest stratum, the guenon's smaller body size may have forced them to make decisions regarding alternative locomotor behaviors quite frequently. Further, their ability to use a larger subset of understory supports afforded them a wider range of locomotor options when crossing breaks in vegetation. The presumed greater level of feeding competition associated with their more frugivorous/insectivorous diet may have selected for expediency of locomotion (i.e., fastest travel possible to a desired feeding location) over any other preference. In other words, if guenon food resources were limited in southern forest (i.e., harder to find in the dense vegetation, more energetically taxing to acquire in the flexible understory, less available due to habitat disturbance), then guenons may have engaged in whatever locomotor behavior enabled them to outcompete conspecifics. Whether differences in diet or forest structure were the driving cause of intraspecific locomotor differences in guenons remains unclear. In either case, contrasts in body size and locomotor adaptations between the two species likely facilitated locomotor plasticity in guenons but constrained locomotor profiles in colobus.

Guenons can and do change locomotor profiles in differing forest habitats. I have suggested that differences in forest architecture between southern and western forest at BFMS played a crucial role in producing this intraspecific variation. However, differences in feeding competition, population density, social interactions, etc. between these forests may have also played a role in producing intraspecific variation. Only more detailed intraspecific comparisons of social and
dietary behavior can determine how significant the influence of any of these factors might have been on guenon locomotor variation.

Regardless of what drives this behavioral variation, the fact that locomotor profiles are variable is important for understanding and posing new questions regarding the socioecology of these two guenon groups. Mammides et al. (2008) illustrated that to accurately judge the risks that habitat disturbance might pose to primate species, we need to account for not just total abundance of what we perceive as food resources but also the distribution and diversity of those resources. In that sense, these locomotor differences will hopefully encourage future researchers to identify and protect those resources and arboreal pathways that guenons in more disturbed forest rely on for their survival.

Does the plasticity of guenon locomotion displayed in this study bring into question the conservative nature of primate positional behavior identified in previous studies (e.g., Doran and Hunt, 1994; Garber and Pruetz, 1995; McGraw 1996b)? For colobus, locomotor profiles remained statistically identical despite significant differences in habitat use and posture. For guenons, differences in locomotor profiles were statistically significant but nevertheless quite subtle. There were no clear differences in the ranked preference of locomotor behaviors between the two guenon groups (Table 7.10). All female guenons engaged most frequently in Quadrupedalism followed by very similar frequencies of Leap and Horizontal Climb. Vertical Climb was infrequently exhibited and Drop was extremely rare. Despite intraspecific variation in the frequency of several locomotor behaviors, both guenon
groups consistently preferred some behaviors to others. This study suggests that while slight frequency differences in locomotor behaviors may be associated with habitat disturbance and might elicit important behavioral information regarding a primate’s day-to-day locomotor strategies, these differences are insufficient to cast doubt on established form-function associations in living primates.

<table>
<thead>
<tr>
<th>Ranked Guenon Locomotor Behaviors (From Most Common to Least Common)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Quadrupedalism</td>
</tr>
<tr>
<td>2. Leap or Horizontal Climb*</td>
</tr>
<tr>
<td>3. Leap or Horizontal Climb*</td>
</tr>
<tr>
<td>4. Vertical Climb</td>
</tr>
<tr>
<td>5. Drop</td>
</tr>
</tbody>
</table>

**Table 7.10: Ranked Preference of Locomotor Behaviors for *C. campbelli lowei.*** This table ranks locomotor behaviors by their frequency (highest to lowest) for both guenon groups. *Periphery Guenons and Central Guenons both engaged in Leap and Horizontal Climb behaviors during Non-Social Locomotion at very similar frequencies. Differences were so minute as to obscure any clear preference in either guenon group for one locomotor behavior over the other.

**Conclusion**

In this chapter, I compared locomotor profiles of *C. vellerosus* and *C. campbelli lowei* inhabiting structurally distinct forest habitats at Boabeng-Fiema Monkey Sanctuary, Ghana. I tested whether differences in forest architecture and habitat usage profiles were sufficient to produce differences in the frequency that each species adopted specific locomotor behaviors in highly disturbed southern forest. The results of this test are summarized below:
1. Colobus exhibited no significant intraspecific differences in overall locomotor patterns between forest types. However, the paucity of large supports at low heights and the reduced number of upper canopy arboreal pathways in disturbed southern forest influenced the vertical distribution of locomotor behaviors for female Redtail Colobus found there.

2. Female guenons in more disturbed southern forest (Periphery Guenons) differed in their overall locomotor profiles from female guenons in less disturbed western forest (Central Guenons). These locomotor contrasts were driven by differences during Non-Social Locomotion (i.e., movement during foraging and travel).

3. Increased frequencies of Leap and Horizontal Climb in Periphery Guenons are likely responses to the flexible, dense, and heterogeneous nature of disturbed southern forest understory. Periphery Guenon females engaged in Quadrupedalism less frequently in disturbed southern forest as predicted, however, it is notable that Quadrupedalism was nevertheless used within all forest strata.

4. Body size differences may, at least in part, explain why guenons varied in their locomotor profiles to a greater degree than did colobus. Guenons may have encountered more breaks in the canopy and likely had more locomotor options than did colobus in crossing and/or circumnavigating those breaks. Further, colobus leaping adaptations may have constrained them to engage
in locomotor behaviors (e.g., Leaps, bounding Quadrupedalism) that this morphology easily facilitated.
Chapter 8: Intraspecific Sex Differences

Given male-female differences in body mass, the nutritional costs of reproduction, social dominance, access to resources, and the role of adult males and females in infant care and protection, sex-based differences in positional behavior are expected. (Garber, 2007, p. 552)

Introduction

In previous chapters, I tested whether the frequencies at which *C. vellerosus* and *C. campbelli lowei* engaged in postures or locomotor behaviors varied as a response to the nature of forest architecture in two forest areas at BFMS. I demonstrated that habitat usage profiles and postural profiles varied between forest types for both species. Further, I demonstrated that locomotor behavior differed for *C. campbelli lowei* but not for *C. vellerosus*. Despite the potential ecological significance of these statistically significant intraspecific differences, I argued that the subtle differences exhibited in the intraspecific comparisons supports the hypothesis that these primate species largely conserve their positional behavior irrespective of habitat. In other words, these results cast very little doubt on the notion, vital to establishing accurate form-function associations, that primates exhibit consistent postural or locomotor profiles even in starkly different forest habitats.

Intraspecific sex differences in positional behavior, however, pose another challenge to establishing these form-function associations. If substantial positional
behavior differences exist between males and females of a species, then that would imply that a single positional behavior profile for that species might be inappropriate and that sex-specific profiles may be more informative. Doran (1993) emphasized the significance of identifying sex differences in positional behavior, particularly in the context of using extant primates as models for inferring behavior from fossil remains. She argued that the presence of extensive variation in the positional behavior of sexually dimorphic living species might have important implications for contrasting sex-based behavioral patterns of our early hominid relatives. It is possible, for example, that if intraspecific morphological differences can be tied to intraspecific differences in behavior for males and females in living species, then such associations could shed light on differing male and female roles in extinct primate communities (i.e., the roles of each sex in foraging, territorial defense, etc.). Differentiating male and female positional behavior patterns in living species is therefore important not just for understanding modern behavioral variation, but also for offering new avenues of inquiry into the lifeways of past species.

As the introductory quote for this chapter suggests, many have assumed that because differences in biology (i.e., body size, reproductive demands, etc.) and behavior (i.e., territorial defense, offspring protection and transport, etc.) exist between male and female primates, sex-based differences in positional behavior may exist as well. However, primate field researchers have identified few intraspecific sex-based differences. Doran (1993) compared the postural and
locomotor strategies of adult chimpanzees \( (Pan\ troglodytes) \) under the assumption that body size dimorphism would place greater limitations on support availability for males than females. Doran (1993) did identify significant sex differences in the locomotor behavior during travel within feeding trees (i.e., females moved quadrupedally more often than males). Since total arboreal feeding time in Doran’s (1993) study accounted for only 2.2% of positional behavior observations, Garber (2007) characterized these differences as “extremely subtle.” Travel overall and travel between feeding trees, however, did not produce significant intraspecific differences between chimpanzee sexes. Doran (1993) argued that locomotor differences were not found during these activities due to the fact that both males and females spent the majority of their travel time knuckle-walking on the ground. Doran (1993) also found significant postural differences during male/female resting periods (i.e., males lie more frequently and females sit more frequently) and associated those differences primarily with support choice (i.e., males choosing larger supports than females).

Significant biologically and/or ecologically based sex differences in positional behavior remain elusive as most studies do not show clear, consistent trends across the primate order. For New World monkeys, Gebo (1992) noted that the mantled howler \( (Alouatta\ palliata) \) exhibited “virtually identical locomotor frequencies for all varieties of movement” (p. 282) during travel with very minor differences (i.e., more climbing and less quadrupedalism by females) during foraging. For the white-throated capuchin \( (Cebus\ capucinus) \), Gebo (1992) found a similar pattern with
greater climbing in females and greater quadrupedalism in males. These differences were substantial for capuchins, amounting to an almost 10% difference (quadrupedalism: males 58%, females 49%; climbing: males 22%, females 29%) and much subtler for howlers (quadrupedalism: males 48%, females 45%; climbing: males 35%, females 38%). In neither case did overall locomotor patterns change with both species exhibiting the same ranked preference of locomotor behaviors. The fact that Gebo (1992) applied no statistical tests to these data make their interpretation challenging and Bezanson (2006) found no significant sex differences in positional behavior for either *C. capucinus* or *A. palliata*.

Though few studies have examined sex-differences in Old World monkey positional behavior, Gebo and Chapman (1995a) found an average of only 2% difference in locomotor behavior between males and females for five sexually dimorphic species (three guenons and two colobus) in the Kibale Forest Reserve of Uganda. When constrained by maintenance activity, sex-based variation was only slightly greater and never in excess of 4%. Overall, the authors stated that “no appreciable locomotor differences can be documented between males and females in these sexually dimorphic species, even though the sexes clearly differ in their respective body sizes” (pp. 56–57). They further recorded minimal intraspecific differences in the use of supports varying in size, orientations and heights.

Researchers typically rely on body size dimorphism, intraspecific behavioral differences, or a combination of the two to explain any observed positional behavior differences (Gebo, 1992; Doran, 1993; Chatani, 2003). For example, Chatani (2003)
found that the larger Japanese macaque (*Macaca fuscata*) males relied on a more variable locomotor repertoire, including higher percentages of leaping, scrambling, and bridging, than females. Posturally, males were found to sit less and lie more than did females. Chatani (2003) compared his data to predictions associated with body size dimorphism and argued that his observations could be better explained by sex-based differences in social behavior. Chatani (2003) argued that males use more direct routes (i.e., “shortcuts”) across arboreal substrates than do females in order to maximize the time they can devote to social activities. In contrast, females move more cautiously and indirectly, perhaps to protect infants still reliant on their mother’s transportation from the risks of gap-crossing behavior. Chatani (2003) also identified sex-based postural differences. Females engaged in sit postures more frequently and lie postures less frequently than males. He suggested that these postural differences stem from the fact that females more frequently groom other group members (particularly their own infants) than do males. In both of these examples, Chatani (2003) used differing social roles of males and females rather than differences in body mass to explain Japanese macaque positional behavior variation.

The factors underlying potential sex-based differences in positional behavior are numerous and make explaining this multivariate problem challenging. In this chapter, I compare male and female postures and locomotor behaviors for *C. vellerosus* and *C. campbelli lowei* at BFMS in the less disturbed western forest (i.e., Wawa Colobus and Central Guenons) to identify differences in overall
postural/locomotor profiles or postural/locomotor profiles in the context of
different maintenance activities.

**Hypotheses**

- *Research Question:* Do male and female colobus and/or guenons differ in
  their use of postures and locomotor behaviors at BFMS?

Given the variety of differences that distinguish the daily activities of male
and female primates, one might assume that the sexes would exhibit substantial
intraspecific differences in positional behavior. I present predictions and expected
postural/locomotor changes for each of the study species separately (*C. vellerosus:*
Table 8.1; *C. campbelli lowei:* Table 8.2.). Justifications for these predictions are
presented below.
<table>
<thead>
<tr>
<th>Colobus Predictions</th>
<th>Predicted Cause of Sex Differences</th>
<th>Expected Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₀</td>
<td>Conservative nature of positional behavior</td>
<td>- No change; male/female locomotion and posture remain identical</td>
</tr>
<tr>
<td>H₁</td>
<td>Sexual dimorphism in body mass will restrict behaviors on certain supports</td>
<td>- Males will engage in <em>Horizontal Climb</em> at higher frequencies and <em>Leap</em> and <em>Quadrupedalism</em> at lower frequencies than females</td>
</tr>
<tr>
<td>H₂</td>
<td>Differences in dietary requirements require females to feed more frequently</td>
<td>- Females will <em>Sit</em> more frequently and <em>Recline</em> less frequently than males</td>
</tr>
<tr>
<td>H₃</td>
<td>Differences in vigilance behavior require males to more actively patrol territories and exhibit dominance behavior</td>
<td>- Males will <em>Sit</em> more frequently and <em>Recline</em> less frequently than females - Males engage in higher frequencies of <em>Leap</em> and <em>Quadrupedalism</em> than females</td>
</tr>
</tbody>
</table>

Table 8.1: Predictions for Sex-based Differences in Wawa Colobus Positional Behavior.

<table>
<thead>
<tr>
<th>Guenon Predictions</th>
<th>Predicted Cause of Sex Differences</th>
<th>Expected Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₀</td>
<td>Conservative nature of positional behavior</td>
<td>- No change; male/female locomotion and posture remain identical</td>
</tr>
<tr>
<td>H₁</td>
<td>Sexual dimorphism in body mass will restrict behaviors on certain supports</td>
<td>- Males will exhibit higher <em>Horizontal Climb</em> frequencies and lower <em>Leap</em> and <em>Quadrupedalism</em> frequencies than females</td>
</tr>
<tr>
<td>H₂</td>
<td>Differences in dietary requirements require females to feed more frequently</td>
<td>- Females will <em>Stand</em> more frequently and <em>Recline</em> less frequently than males - Females will <em>Horizontal Climb</em> and <em>Leap</em> at higher frequencies than males</td>
</tr>
<tr>
<td>H₃</td>
<td>Differences in vigilance behavior force males to more actively patrol territories and exhibit dominance behavior</td>
<td>- Males will <em>Sit</em> more frequently and <em>Recline</em> less frequently than females - Females will <em>Leap</em> and <em>Horizontal Climb</em> at higher frequencies than males</td>
</tr>
</tbody>
</table>

Table 8.2: Predictions for Sex-based Differences in Guenon Positional Behavior.

H₀ proposes that there will be no significant differences between males and female postural or locomotor profiles for either colobus or guenons at BFMS. After reviewing literature comparing male and female positional behavior in apes and
monkeys, Garber (2007) concluded that “taken together, the data...provide only limited evidence for significant sex-based differences in locomotion, posture, and substrate utilization” (p. 554). Several other researchers have noted consistent postural and locomotor patterns between male and female primates (Gebo and Chapman, 1995a; Bezanson, 2005) and even those that have identified intraspecific sex differences in either posture or locomotion (Gebo, 1992; Doran, 1993; Chatani, 2003) regard such differences as surprisingly minimal given often dramatic differences in body size. $H_0$ then predicts that neither body size differences nor contrasting social roles will be sufficient to produce significant differences in positional behavior profiles for either monkey species at BFMS.

Much as Fleagle (1980, 1985) argued in the context of interspecific differences in positional behavior, Doran (1993) suggested that body size dimorphism in some nonhuman primate species may be significant enough to result in different postural and locomotor profiles between males and females. Owing to their larger body size, males may be more restricted by the types of supports capable of bearing their weight and may encounter fewer canopy gaps than would females. Doran (1993) found that male chimpanzees, while traveling between supports within a feeding tree, were forced to use a more variable locomotor repertoire (e.g., more climbing) due the fact that smaller branches in the tree crown periphery limited the larger male’s ability to utilize quadrupedalism. Male and female C. vellerosus and C. campbelli lowei differ in body size (Table 8.3). Assuming that body size dimorphism is driving any intraspecific differences in positional
behavior at BFMS, \( H_1 \) predicts that male colobus and male guenons will engage in both \textit{Leaps} and \textit{Quadrupedalism} less frequently than do females. Since suspensory behavior is unexpected in either species, \textit{Horizontal Climb} frequencies may also increase in males as a possible alternative locomotor strategy.

<table>
<thead>
<tr>
<th>Species</th>
<th>Male Range</th>
<th>Male Average</th>
<th>Female Range</th>
<th>Female Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{C. vellerosus}</td>
<td>8000–9100g (17.64–20.06lbs)</td>
<td>8500g (18.74lbs)</td>
<td>6200–7500g (13.66–16.53lbs)</td>
<td>6860g (15.12lbs)</td>
</tr>
<tr>
<td>\textit{C. campbelli lowei}</td>
<td>3200–4600g (7.05–10.14lbs)</td>
<td>3884g (8.56lbs)</td>
<td>1800–5000g (3.97–11.36lbs)</td>
<td>2563g (5.65lbs)</td>
</tr>
</tbody>
</table>

\textbf{Table 8.3: Male and Female Body Mass for \textit{C. vellerosus} and \textit{C. campbelli lowei}.} These measures are not derived from the BFMS study populations but were collected from curated specimens by Delson et al. (2000).

Both \( H_2 \) and \( H_3 \) predict that behavioral differences (e.g., diet, vigilance) will drive differences in positional behavior at BFMS. \( H_2 \) predicts that dietary stress is the primary cause of intraspecific sex differences. Gebo (1992) suggested that if females are under greater dietary stress due to the increased energetic demands associated with pregnancy and lactation, they may be required to utilize locomotor or postural behaviors that allow them access to greater quantities of food and/or higher quality food items. Even among highly folivorous primates, females may exhibit increased dietary demands and a great deal of feeding competition if resources are sparsely distributed (Koenig et al., 1998). Gebo (1992) suggested that females might mitigate some of this feeding competition by either feeding more often in the most productive forest strata and/or actively avoiding competition with dominant males. At BFMS, \( H_2 \) predicts that the more folivorous female colobus will
engage in higher frequencies of *Horizontal Climb* as they move throughout the periphery of tree crowns in search of leaves. This may allow them increased access to leaf resources from which males are less able, due to their larger body size, to displace them. Female colobus are predicted to engage in *Sit*, a typical posture for “banqueters” (Oates, 1987), at a higher frequency than do male colobus as they place themselves within reach of large leaf bunches. In contrast, the more insectivorous/frugivorous female guenons will likely exhibit higher frequencies of *Stand* postures as they scan the understory for rarer food items (i.e., insects, fruit) and higher frequencies of *Horizontal Climb* and *Leap* as they compete to reach these more patchily distributed resources (Garber, 1987; Oates, 1987).

H₃ predicts that social responsibilities and relationships rather than diet will drive any positional behavior differences. If social behaviors vary between species at BFMS, the nature of their influence over positional behavior might also vary. For example, male colobus and male guenons at BFMS regularly scanned for extragroup males or nearby groups but differ dramatically in their approach to intergroup conflicts and in their social displays. Male colobus tended to become directly involved in chases and physical conflict between groups or while defending their territory or dominance rank from competing males. Females were less likely than males to become the aggressor in these activities. Guenon conflicts, in contrast, were much different. Female guenons were the main participants in conflicts, grouping together and participating as a unit in a series of lunges and retreats against other groups. The tendency for female participation in intergroup conflicts is common in
several guenon species (Cords, 1987). These conflicts can be quite violent with mobs of females inflicting potentially mortal wounds using their canines (McGraw et al., 2002). Like many guenon species (Cords, 1987), *C. campbelli lowei* males rarely became directly involved in conflicts, preferring instead to climb above physical confrontations and threaten opposing males through their postures (e.g., legs spread, series of head-bobs, forceful arm raises) and vocalizations.

Additionally, male colobus and male guenons differed in their social displays. Primate vocalizations may serve several functions including predator detection and avoidance (e.g., Zuberbuler, 2001), maintenance of intra/intergroup spacing over long distances (e.g., Mitani and Stuht, 1998) and vocal indication of individual male status (Kitchen et al., 2003). Male black-and-white colobus produce loud calls known as roars that often occur in conjunction with rapid leaps between large supports (Oates and Trocco, 1983). At BFMS, male *C. vellerosus* would often make loud calls in response to nearby males while bounding and leaping between large arboreal Boughs high in the canopy. These displays were often followed by *Recline* or *Sit* postures near female group members that subsequently groomed the displaying male. Alternately, lower ranking males might *Sit* along the periphery of the group to maintain visual sight of nearby groups. In contrast, male guenons produce booming loud calls, audible from great distance, that are thought to be associated with group cohesion (Gautier, 1988) and/or as an indicator of male quality (Zuberbuhler, 2004). At BFMS, *C. campbelli lowei* males also regularly made territorial calls. Unlike the loud calls of male colobus, male guenon loud calls were
rarely associated with other physically active forms of display (e.g., leaping, branch-shaking). Instead, male guenons would typically move to a location, Sit or even at times Recline, and loud call repeatedly. These calls often, but not always, occurred when two guenon groups came in close proximity to one another.

Given these behavioral differences between species, H₃ posits different predictions regarding the nature of sex-based intraspecific differences in positional behaviors for C. vellerosus and C. campbelli lowei. For colobus, H₃ predicts that some element of male positional behavior is driven by the male’s role in home range surveillance and territorial defense. While positioning themselves so they are better able to react to approaching threats and monitor their surroundings, male colobus are predicted to engage in Sit more frequently and Recline less frequently than females. Male colobus may also use more direct travel routes to conserve energy for intergroup conflicts and better position themselves for group defense. If true, male colobus will engage in Quadrupedalism more frequently than females whenever direct pathways are available and Leap behaviors more frequently to cross canopy gaps when direct pathways are unavailable.

Similarly, male guenons, as they scan for group threats and/or observe social conflicts, are expected to engage in Sit postures more frequently than are female guenons. In Chapter 5, I found that guenons spent a larger proportion of their time in the understory than in other forest strata. If social roles associated with intergroup conflict and group defense are driving intraspecific positional behavior differences in guenons, I predict that female guenons involved more directly in
territorial defense will engage in higher frequencies of *Leap* and *Horizontal Climb* than males. This is because females are predicted to more frequently chase or retreat from opposing females throughout the forest understory.

**Methods**

To compare male and female postural and locomotor profiles at BFMS, I used the instantaneous three-minute focal sampling technique described in Chapter 4. I have argued that intraspecific differences in postural profiles for both species and locomotor profiles for guenons are related to differences in the nature of forest architecture between southern and western forests at BFMS. I have also argued that forest architecture in southern forest was substantially disturbed, forcing both species to use the lowest forest strata at a higher frequency than did conspecifics in western forest. Given these facts, it would be inappropriate to pool all male and all female positional behavior for each species. Since western forest is less disturbed, I opted to compare positional behavior profiles only for males and females of each species found there. For colobus this included the males and females of Wawa Colobus group. For guenons this included the males and females of both groups composing the Central Guenons (see Chapter 3 for a description of these groups and their ranges).

I spent the first week prior to the observational portion of this study familiarizing myself with both study groups. For guenons, sex differences were immediately apparent from a number of cues (Figure 8.1). First, intraspecific
differences in body mass and body proportions were clear from visual observation. Males appeared both larger in overall body size and more robust in facial features and in the torso and upper limbs than were females. Female guenon nipples were bright pink and readily visible against their white fur, further distinguishing the sexes.

![Image of male and female guenons.](image)

**Figure 8.1: Visual Differences between Male and Female Guenons.** The male pictured on the left, like all alpha males, was characterized by a wide face, large torso and robust limbs. The female on the right was thinner and smaller. All fully adult females exhibited elongated nipples whose pink coloration stood out starkly against the white fur on their chest.

For colobus, sexing by visual observation between rapid focal samples was more difficult (Figure 8.2). Body size differences were only readily apparent when male and female individuals were in close proximity to one another. When monkeys were high in the canopy, it became necessary to use additional visual cues. Male colobus faces appeared broader with a rounded projecting jaw. When visible, the
male’s pink penis was readily apparent against his black testicles and fur. The female colobus’ dark nipples were harder to identify from a distance though close proximity to infants was often a clue to a focal animal’s sex. Finally, a slight variation in the patterning of the grey and black fur along the rump distinguished males from females.

Figure 8.2: Visual Differences between Male and Female Colobus. Males, like the one pictured on the left, exhibited more projecting, rounded faces than females (right). The proximity of offspring or visible genitals/nipples offered further clues to the focal animal’s sex.

Studying sex differences in primate groups where females outnumber males by a substantial margin poses significant practical challenges. This was the case for both the colobus and guenon groups. The Wawa Colobus group included several adult males. Every attempt was made to distinguish subadult male colobus from adult females but occasional misattributions were possible. Both guenon groups that comprised the Central Guenons included only one single fully adult male and
there were no subadults large enough to approximate either male or female adult body size. As a result of the self-imposed limitations set on repeated sampling in this study, I recorded fewer male samples than female samples for both species. How this may have affected or biased intraspecific comparisons is unclear. Male samples may be biased to those periods when males were in close proximity to the group. For colobus, this was the case for the majority of observation periods but for guenons, males frequently moved away from other group members, often for long periods of the day. As such, any significant intraspecific sex differences between postural and locomotor profiles must be considered in the context of a limited and potentially biased sample size.

Results

I compared profiles for all postures and all locomotor behaviors between the sexes in western forest using Row x Column tests of independence. For both colobus and guenons at BFMS, posture/locomotion and sex exhibited a dependent relationship (Table 8.4). In other words, overall postural and locomotor profiles for males and females of both species differed in western forest at BFMS. The results of these comparisons are presented below.
<table>
<thead>
<tr>
<th>Species/Group</th>
<th>Posture and Sex</th>
<th>Locomotion and Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus</td>
<td>G-test: 11.879; p=0.003</td>
<td>G-test: 12.036; p=0.034</td>
</tr>
<tr>
<td>Central Guenons</td>
<td>G-test: 25.085; p&lt;0.000</td>
<td>G-test: 14.771; p=0.011</td>
</tr>
</tbody>
</table>

Table 8.4: Results of Sex-based Intraspecific Comparisons of Postural and Locomotor Profiles for Guenons and Colobus in Unlogged Western Forest. Each result fell below the 0.05 significance threshold indicating that males and females of both species differed in their overall postural and locomotor frequencies in western forest.

*C. vellerosus:*

Wawa Colobus males differed significantly from females in their overall postural profiles (Table 8.5, Figure 8.3). Both males and females engaged in *Sit* far more frequently than they engaged in *Recline*; however, female Wawa Colobus sat approximately 3% less frequently and reclined approximately 3% more frequently than did males. Despite substantial differences in the total number of female and male observations, all postures grouped into the *Other* category (e.g., Forelimb Suspend, Stand, Vertical Cling) accounted for an identical proportion (0.6%) of overall postural profiles for both colobus sexes.
<table>
<thead>
<tr>
<th>Sex</th>
<th>Recline</th>
<th>Sit</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>12.1%</td>
<td>87.4%</td>
<td>0.6%</td>
<td>4232</td>
</tr>
<tr>
<td>Male</td>
<td>8.6%</td>
<td>90.8%</td>
<td>0.6%</td>
<td>1200</td>
</tr>
</tbody>
</table>

Table 8.5: Overall Postural Profiles for Male and Female Wawa Colobus.

![Wawa Colobus: Postural Frequencies](image)

Figure 8.3: Comparison of All Postural Behaviors for Male and Female Wawa Colobus.

Male overall locomotor profiles differed from female locomotor profiles significantly for colobus as well (Table 8.6; Figure 8.4). The clearest differences between the sexes in the overall locomotor profiles were between *Leap* and *Horizontal Climb* frequencies. Male *Leap* frequencies were more than 10% higher than those of females while male frequencies of *Horizontal Climb* were nearly 10% lower. Females engaged in *Quadrupedalism* approximately 3% more frequently than did males. Frequencies of *Vertical Climb* were very similar between the two sexes. *Drop* and *Other* locomotor behaviors accounted collectively for 4% or less of all
locomotion for both male and female Wawa Colobus. Differences in the frequencies of Drops were minimal (<1%) and Other locomotor behavioral frequencies were identical.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Drop</th>
<th>Leap</th>
<th>Horizontal Climb</th>
<th>Quad.</th>
<th>Vertical Climb</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>1.8%</td>
<td>33.3%</td>
<td>20.0%</td>
<td>33.5%</td>
<td>9.9%</td>
<td>1.5%</td>
<td>669</td>
</tr>
<tr>
<td>Male</td>
<td>2.5%</td>
<td>44.2%</td>
<td>11.8%</td>
<td>30.9%</td>
<td>9.3%</td>
<td>1.5%</td>
<td>204</td>
</tr>
</tbody>
</table>

Table 8.6: Overall Locomotor Profiles for Male and Female Wawa Colobus.

![Wawa Colobus: Locomotion](image)

Figure 8.4: Comparison of All Male and Female Locomotor Behaviors for Wawa Colobus.

Intraspecific comparisons of positional behavior by sex during each of the maintenance activities used in these study are presented in Table 8.7. These comparisons reduced sample size substantially. As such, no Row x Column statistical tests were used to compare individual postures during maintenance activities.
Instead, these data are provided primarily to illustrate which maintenance activities may have driven overall postural and locomotor differences between the sexes.

<table>
<thead>
<tr>
<th>Postural Maintenance Activities</th>
<th>S</th>
<th>Recline</th>
<th>Sit</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active Feed</td>
<td>F</td>
<td>0.3%</td>
<td>98.1%</td>
<td>1.6%</td>
</tr>
<tr>
<td></td>
<td>(3)</td>
<td>(914)</td>
<td>(15)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>0%</td>
<td>99.1%</td>
<td>0.9%</td>
</tr>
<tr>
<td></td>
<td>(0)</td>
<td>(230)</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Food Processing</td>
<td>F</td>
<td>0%</td>
<td>41.7%</td>
<td>58.3%</td>
</tr>
<tr>
<td></td>
<td>(0)</td>
<td>(5)</td>
<td>(7)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>0%</td>
<td>0%</td>
<td>100%</td>
</tr>
<tr>
<td></td>
<td>(0)</td>
<td>(0)</td>
<td>(3)</td>
<td></td>
</tr>
<tr>
<td>Rest</td>
<td>F</td>
<td>15.2%</td>
<td>84.7%</td>
<td>0.1%</td>
</tr>
<tr>
<td></td>
<td>(483)</td>
<td>(2687)</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>10.5%</td>
<td>89.3%</td>
<td>0.2%</td>
</tr>
<tr>
<td></td>
<td>(99)</td>
<td>(845)</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>Rest Feed</td>
<td>F</td>
<td>0%</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>(0)</td>
<td>(13)</td>
<td>(0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>0%</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>(0)</td>
<td>(2)</td>
<td>(0)</td>
<td></td>
</tr>
<tr>
<td>Rest Social</td>
<td>F</td>
<td>23.3%</td>
<td>76.7%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>(24)</td>
<td>(79)</td>
<td>(0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>23.5%</td>
<td>76.5%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td>(4)</td>
<td>(13)</td>
<td>(0)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Locomotor Maintenance Activities</th>
<th>S</th>
<th>Drop</th>
<th>Leap</th>
<th>Horizontal Climb</th>
<th>Quadrupedalism</th>
<th>Vertical Climb</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Social Locomotion</td>
<td>F</td>
<td>1.7%</td>
<td>33.4%</td>
<td>20.1%</td>
<td>33.3%</td>
<td>10.0%</td>
<td>1.5%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(11)</td>
<td>(220)</td>
<td>(132)</td>
<td>(219)</td>
<td>(66)</td>
<td>(10)</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>2.4%</td>
<td>39.3%</td>
<td>13.1%</td>
<td>33.3%</td>
<td>10.7%</td>
<td>1.2%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(4)</td>
<td>(66)</td>
<td>(22)</td>
<td>(56)</td>
<td>(18)</td>
<td>(2)</td>
</tr>
<tr>
<td>Social Locomotion</td>
<td>F</td>
<td>9.1%</td>
<td>27.3%</td>
<td>18.2%</td>
<td>45.5%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1)</td>
<td>(3)</td>
<td>(2)</td>
<td>(5)</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>2.8%</td>
<td>66.7%</td>
<td>5.6%</td>
<td>19.4%</td>
<td>2.8%</td>
<td>2.8%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1)</td>
<td>(24)</td>
<td>(2)</td>
<td>(7)</td>
<td>(1)</td>
<td>(1)</td>
</tr>
</tbody>
</table>

Table 8.7: Positional Behavior of Male and Female Wawa Colobus During Seven Maintenance Activities. In parentheses under each of these frequencies, I list the total number of observations for that behavior. No statistical tests were used to compare these frequencies due to small male sample sizes.
For Wawa Colobus, Rest was by far the most frequently observed postural activity with more than twice as many observations as Active Feed, the next most commonly observed maintenance activity. Rest Social activities were far less common than either Rest or Active Feed. Food Processing and Rest Feed were maintenance activities I very rarely observed for Wawa Colobus. Neither was observed more than 3 times for male colobus. Note that during the two most frequently observed activities, Rest and Active Feed, sex differences in posture were consistent with overall postural differences (i.e., males sitting at higher frequencies reclining at lower frequencies than females). During Rest Social, differences in the frequencies of Sit and Recline postures between the sexes are extremely small (0.2% for both). Postural frequency differences for Active Feed are also fairly small with the greatest difference (1%) being associated with male and female frequencies of the Sit posture. Being the most common maintenance activity and exhibiting the highest frequency differences between postures, it seems likely that those postures adopted during Rest drove the significant overall differences in male and female postural profiles for Wawa Colobus.

For both male and female Wawa Colobus, the profile for all locomotor behaviors is dominated by those locomotor behaviors occurring during Non-Social Locomotion. For females, Non-Social Locomotion accounted for more than 96% of all locomotor behaviors (648 out of 669 total observations of female Wawa Colobus locomotion). For males, Non-Social Locomotion accounted for more than 82% of all locomotor behaviors (168 out of 204 total observations of male Wawa Colobus locomotion).
locomotion). The most striking contrasts between the sexes in the frequencies of any specific Non-Social Locomotion behavior are in *Horizontal Climb, Leap, and Quadrupedalism*. Male Wawa Colobus leapt at more than twice the frequency of females during Social Locomotion and nearly 6% more frequently than did females during Non-Social Locomotion. During Social Locomotion, females exhibited a more than 10% greater frequency of *Horizontal Climb* than males and moved via *Quadrupedalism* at a more than 20% higher frequency. During Non-Social Locomotion, *Horizontal Climb* frequencies remained higher in females by 7% but frequencies of *Quadrupedalism* were identical between the sexes.

*C. campbelli lowei*:

Male and Female Central Guenons also differed significantly in overall postural profiles (Table 8.8, Figure 8.5). For both male and female Central Guenons, *Sit* postures accounted for more than 80% of all observed postures. The next most common posture for both sexes was *Stand* followed by *Recline*. Male guenons engaged in *Sit* postures 5% more frequently than females and *Recline* postures nearly 2% more frequently than females. In contrast, female Central Guenons adopted *Stand* postures at frequencies nearly 6% higher than those of males. Neither sex relied heavily on *Cling* or *Other* postures, both accounting for less than 2% of all observed postures.
<table>
<thead>
<tr>
<th>Sex</th>
<th>Cling</th>
<th>Recline</th>
<th>Sit</th>
<th>Stand</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>0.9%</td>
<td>3.2%</td>
<td>80.2%</td>
<td>15.2%</td>
<td>0.4%</td>
<td>3153</td>
</tr>
<tr>
<td>Male</td>
<td>0.2%</td>
<td>5.1%</td>
<td>85.3%</td>
<td>9.3%</td>
<td>0.2%</td>
<td>590</td>
</tr>
</tbody>
</table>

Table 8.8: Overall Postural Profiles for Male and Female Central Guenons.

Figure 8.5: Comparison of All Postures for Male and Female Central Guenons.

Locomotor profiles also differed between male and female Central Guenons (Table 8.9, Figure 8.6). The Quadrupedalism and Horizontal Climb locomotor behaviors accounted for the highest frequency differences between male and female guenons. Guenon males engaged in Quadrupedalism greater than 10% more frequently than did guenon females. Conversely, guenon females engaged in Horizontal Climb more frequently than males and at approximately the same percentage. Rates of Leap, Drop, and Other postures were very similar between the
guenon sexes. *Vertical Climb* exhibited a slight sex difference (<2%) in favor of females.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Drop</th>
<th>Horizontal Climb</th>
<th>Leap</th>
<th>Quad</th>
<th>Vertical Climb</th>
<th>Other</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>1.2%</td>
<td>19.3%</td>
<td>21.1%</td>
<td>49.7%</td>
<td>7.1%</td>
<td>1.6%</td>
<td>1459</td>
</tr>
<tr>
<td>Male</td>
<td>1.1%</td>
<td>9.4%</td>
<td>22.7%</td>
<td>60.2%</td>
<td>5.5%</td>
<td>1.1%</td>
<td>181</td>
</tr>
</tbody>
</table>

Table 8.9: Overall Locomotor Profiles for Male and Female Central Guenons.

![Central Guenons: Locomotion](image)

Figure 8.6: Comparison of All Male and Female Locomotor Behaviors for Central Guenons.

I compared male and female guenon use of postures and locomotor categories in the context of each of the seven maintenance activities recorded in this study (Table 8.10). Observations of male guenons were even rarer than those for the colobus resulting in very small male sample sizes for several activities. As a result, no statistical tests were used to compare male and female postural or locomotor
profiles during any particular activity. Instead, these data are presented to illustrate which activities were likely driving overall postural differences and to assess any substantial profile differences between frequently observed activities.

<table>
<thead>
<tr>
<th>Postural Maintenance Activities</th>
<th>S</th>
<th>Cling</th>
<th>Recline</th>
<th>Sit</th>
<th>Stand</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Active Feed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0.3% (1)</td>
<td>0% (0)</td>
<td>67.3% (263)</td>
<td>29.9% (117)</td>
<td>2.6% (10)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>4.8% (1)</td>
<td>0% (0)</td>
<td>81.0% (17)</td>
<td>14.3% (3)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td><strong>Food Processing</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>1.3% (1)</td>
<td>0% (0)</td>
<td>53.2% (42)</td>
<td>41.8% (33)</td>
<td>3.8% (3)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>0% (0)</td>
<td>0% (0)</td>
<td>60.0% (6)</td>
<td>30.0% (3)</td>
<td>10.0% (1)</td>
<td></td>
</tr>
<tr>
<td><strong>Rest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>1.2% (27)</td>
<td>2.8% (64)</td>
<td>82.5% (1856)</td>
<td>13.4% (302)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>0% (0)</td>
<td>4.8% (23)</td>
<td>87.1% (417)</td>
<td>8.1% (39)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td><strong>Rest Feed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0% (0)</td>
<td>0% (0)</td>
<td>98.9% (86)</td>
<td>1.1% (1)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>0% (0)</td>
<td>0% (0)</td>
<td>100% (21)</td>
<td>0% (0)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td><strong>Rest Social</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0% (0)</td>
<td>11.0% (38)</td>
<td>81.3% (283)</td>
<td>7.5% (26)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>0% (0)</td>
<td>11.9% (7)</td>
<td>71.2% (42)</td>
<td>16.9% (10)</td>
<td>0% (0)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Locomotor Maintenance Activities</th>
<th>S</th>
<th>Drop</th>
<th>Leap</th>
<th>Horizontal Climb</th>
<th>Quadrupedalism</th>
<th>Vertical Climb</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Non-Social Locomotion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>1.3% (18)</td>
<td>20.9% (301)</td>
<td>19.6% (282)</td>
<td>49.6% (714)</td>
<td>7.1% (102)</td>
<td>1.6% (23)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>1.1% (2)</td>
<td>22.3% (39)</td>
<td>9.7% (17)</td>
<td>61.1% (107)</td>
<td>5.7% (10)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td><strong>Social Locomotion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>0% (0)</td>
<td>38.9% (7)</td>
<td>0% (0)</td>
<td>55.6% (10)</td>
<td>5.6% (1)</td>
<td>0% (0)</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>0% (0)</td>
<td>33.3% (2)</td>
<td>0% (0)</td>
<td>33.3% (2)</td>
<td>0% (0)</td>
<td>33.3% (2)</td>
<td></td>
</tr>
</tbody>
</table>

Table 8.10: Positional Behavior of Male and Female Central Guenons During Seven Maintenance Activities. In parentheses under each of these frequencies, I list the total number of observations for that behavior. No statistical tests were used to compare these frequencies due to small male sample sizes.
For Central Guenon males and females, Rest was by far the most commonly observed postural activity. Rest postures accounted for approximately 70% of all observed postures for females and approximately 80% of all observed postures for males. Rest Social accounted for nearly 10% of all postures for both sexes. Active Feed was rarely observed for male guenons (21 observations: 3.5%) and more frequently observed for female guenons (391 observations: 12.4%). Postures associated with Food Processing accounted for less than 3% of all observed postures for either sex. During all postural maintenance activities except Rest Social, sex differences in the frequencies of Stand (higher in females), Sit (higher in males), and Recline (higher in males) were consistent with significant sex-based differences in overall postural profiles for Central Guenons. During Rest Social, however, female guenons engaged in Sit postures more than 10% more frequently than males and males engaged in Stand postures 10% more frequently than did females. Recline frequencies during Rest Social differed by less than 1% between the sexes.

Social Locomotion was very rarely observed in either sex (6 observations for males; 18 observations for females). It is unsurprising then that sex differences during Non-Social Locomotion match significant sex-based differences in overall locomotor profiles for Central Guenons. During Non-Social Locomotion, male Central Guenons engaged in Horizontal Climb less frequently and Quadrupedalism more frequently than did females. Both locomotor behaviors differed by approximately the same percentage (~10%). Sex differences in the frequencies of
*Drop, Leap, Vertical Climb,* and *Other* locomotor behaviors during Non-Social Locomotion were comparatively quite small (<2%).

**Discussion**

For both *C. vellerosus* and *C. campbelli lowei,* overall postural and locomotor profiles differed significantly between males and females. I predicted that if statistically significant differences were found, three factors may have played a role in guiding those differences. 1) *Body size* might constrain males to utilize larger supports and/or modify their postural or locomotor profiles to deal with smaller-sized supports. 2) *Increased dietary stress* for females might increase the frequency of postures and locomotor behaviors that can facilitate access to alternate or additional food resources. 3) *Sex differences in social roles,* primarily in regards to territorial defense, might require one sex to more frequently adopt locomotor modes and postures that facilitate both observation and rapid movement across their range. Below, I discuss each of these factors (body size, dietary stress, and social roles) in the context of observed intraspecific postural and locomotor differences for colobus and guenons at BFMS.

*Body Size Drives Male/Female Differences in Positional Behavior*

Larger-bodied primates should be restricted to a smaller subset of those arboreal supports capable of bearing their body weight (Fleagle, 1985). Adult males are larger than adult females in both species at BFMS (Delson et al., 2000). For both
species, *Recline* postures typically occurred on a single support. In contrast, *Sit* postures are highly variable and often allow primates to distribute their body mass across numerous supports (Hunt et al., 1996). Guenons and colobus at BFMS, particularly when they rested atop thinner supports near the ground or in the periphery of tree crowns, often distributed their weight across numerous supports. In Chapter 6, I argued that this may explain why large-bodied female colobus can adopt *Sit* postures during resting or feeding activities even in low-lying, thin, flexible supports.

If body size was the only factor driving postural differences between the sexes in colobus and guenon species at BFMS, we might expect males to have used postures that better support their body weight atop thinner supports. For example, given a hypothetical distribution of supports of varying sizes to which males and females each had equal access, we might expect males to have been able to *Recline* on a smaller proportion of those supports than could females. Colobus males did *Sit* more frequently and *Recline* less frequently than did colobus females. Differences between the sexes for these postures, though statistically significant, were quite subtle (~3%). *Stand* postures, like *Sit* postures, allow larger males to distribute their weight across numerous supports while at Rest. Though colobus rarely *Stand*, guenons frequently do (McGraw, 1998b). However, male guenons engaged in *Sit* and *Recline* postures more frequently than did females and *Stand* postures less frequently.
Locomotor predictions regarding interspecific body size differences were not met for either species. While he focused primarily on explaining interspecific differences in locomotion, Fleagle (1985) predicted that, in identical forests, large-bodied primates would encounter fewer canopy gaps that would need to be crossed through leaping than would smaller-bodied primates. Doran (1993) argued that larger-bodied males in sexually dimorphic species might be expected to Leap less frequently than would females. Additionally, body size might influence above-branch locomotion unrelated to crossing canopy gaps. Though varying in its manner and frequency of use across the primate order, Quadrupedalism is nonetheless a commonly relied upon primate locomotor behavior (Rose, 1993). There is some limited evidence that during some activities (e.g., foraging), larger-bodied males find fewer supports capable of bearing their weight during Quadrupedalism than do females and consequently engage in Quadrupedalism less frequently than do females (Doran, 1993).

I predicted that if males and females were foraging and traveling in structurally identical forest areas/strata, larger-bodied males would engage in Quadrupedalism and Leap behaviors less frequently than females, increasing instead their frequency of alternative locomotor strategies (e.g., Horizontal Climb). However, male colobus engaged in Leap behaviors more frequently than did female colobus. In accordance with Doran (1993), male colobus did engage in Quadrupedalism less frequently than did females however they also engaged in Horizontal Climb less frequently. I identified <1% difference in Leap frequencies between the guenon
sexes. The guenon sexes did differ in rates of *Horizontal Climb* and *Quadrupedalism* but in a manner opposite to that predicted. Female guenons engaged in *Horizontal Climb* at an approximately 10% higher frequency than did males and *Quadrupedalism* 10% less frequently than males.

**Dietary Stress Drives Male/Female Differences in Positional Behavior**

Gebo (1992) suggested that one possible explanation for intraspecific differences in positional behavior between male and female primates might lie with differing dietary requirements. If females required more calories and/or higher quality food resources than males for reproduction and lactation, they might have engaged more frequently in postures or locomotor behaviors that facilitated acquisition of more or better quality foods. The energetic demands of gestation and providing nutrition for offspring are likely exacerbated by the roles mothers play in defending and transporting their offspring. These costs were evident for both female colobus and female guenons. For example, female colobus were highly protective of their young offspring. Females with newborns were very wary of humans and often fled at the slightest hint of potential conspecific or interspecific threats (Figure 8.7). These increased energetic demands, then, could have exerted substantial influence on the positional behavior in either or both species. Due to interspecific dietary differences (colobus: highly folivorous; guenons: highly frugivorous and insectivorous), however, colobus and guenons are unlikely to
exhibit identical intraspecific patterns of postural or locomotor differences between males and females. As such, I discuss results for each species separately below.

Figure 8.7: Female *C. vellerosus* and Infant. Colobus mothers of very young offspring frequently fled when approached by either humans or monkeys from outside their group.

Oates (1987) described folivores as banquet feeders—species that tend to feed from large bunches of leaves at a single location, shifting to new resource locations infrequently. *C. vellerosus* is a highly folivorous primate (Saj et al., 2005; Saj and Sicotte, 2007a) that rarely exhibits *Stand* or suspensory postures (Chapter 6) so it is unsurprising that both male and female colobus in this study engaged in *Sit* as their dominant Active Feed posture (>98% of all postures adopted during Active Feed). If female colobus were feeding more often than male colobus and this
increased feeding frequency drove postural differences between the sexes, we might expect male colobus to have engaged less frequently in *Sit* postures than did females. Instead, I observed the opposite. Males engaged in *Sit* postures more frequently and *Recline* postures less frequently than did females.

**Locomotor** differences between male and female colobus at BFMS better match predictions under the dietary stress hypothesis. While Fleagle (1984) found no clear association between diet and locomotion in primates, McGraw (1998b) argued that the location of preferred food items might greatly influence a primate's postural behavior. This is because the context in which a primate acquires food involves more than the food itself. The size of supports, orientation of supports, presence of canopy gaps, forest density, etc. likely all influence an animal's positional behavior tendencies. Rose (1974) noted that postures often can be conceived of as intermediate stages connecting two locomotor bouts. If posture is influenced by the location of preferred food items, then, locomotion is likely to also be influenced.

Folivorous *C. vellerosus* at BFMS exhibited a clear preference for upper and lower canopy strata (>75% of all observations for Wawa Colobus females in western forest—Chapter 5). Gebo (1992) raised the possibility that female primates under greater dietary stress might avoid being displaced from feeding patches by more dominant members of their groups, particularly alpha males, by exploiting alternate food resources (e.g., food located in strata infrequently visited by dominant individuals). For *C. vellerosus*, those alternative resources might be found outside of
the upper canopy in the lower canopy or understory. Colobus did come to the forest understory to feed frequently. However, the vertical distribution profiles of Active Feed observations were nearly identical for male and female Wawa Colobus (Table 8.11, Figure 8.8). This suggests that females were not specifically selecting resources found in different forest strata.

<table>
<thead>
<tr>
<th>Wawa Colobus: Active Feed</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m–15m</th>
<th>20m+</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>6.7%</td>
<td>30.8%</td>
<td>23.0%</td>
<td>39.6%</td>
<td>932</td>
</tr>
<tr>
<td>Male</td>
<td>6.5%</td>
<td>30.6%</td>
<td>22.8%</td>
<td>40.1%</td>
<td>235</td>
</tr>
</tbody>
</table>

Table 8.11: Forest Strata Profiles for Male and Female Wawa Colobus During Active Feed.

Figure 8.8: Comparison of the Vertical Distribution of Active Feed Observations for Male and Female Wawa Colobus.
It is still possible that females could increase dietary intake by simply feeding more often than males. In the forest understory as well as in the periphery of tree crowns, we might expect colobus to frequently exploit leaf resources located near thinner, arboreal supports. Since locomotion is influenced, at least in part, by support size (McGraw, 1996a, Chapter 7), if female colobus were foraging more frequently than were males, I predicted that females would have engaged in locomotor behaviors that facilitated movement along these smaller, flexible supports. Female colobus did use medium supports (Branches) at a higher frequency and large supports (Boughs) at a lower frequency than did male colobus (Table 8.12, Figure 8.9). They also engaged in Horizontal Climb behaviors nearly twice as frequently as did male colobus (20% vs. 11.8%). Horizontal Climb might be the most effective means of directly traveling between feeding patches using the thinner, discontiguous supports along the periphery of tree crowns as well as between thin, flexible supports in the forest understory.
Table: 8.12: Male and Female Wawa Colobus Support Size Profiles.

<table>
<thead>
<tr>
<th>Wawa Colobus: Locomotion</th>
<th>Ground</th>
<th>Trunk</th>
<th>Bough</th>
<th>Branch</th>
<th>Twig</th>
<th>Vine</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>5.1%</td>
<td>5.7%</td>
<td>42.3%</td>
<td>39.6%</td>
<td>3.6%</td>
<td>0.1%</td>
<td>669</td>
</tr>
<tr>
<td>Male</td>
<td>5.4%</td>
<td>3.9%</td>
<td>54.4%</td>
<td>31.4%</td>
<td>2.4%</td>
<td>1.0%</td>
<td>204</td>
</tr>
</tbody>
</table>

Increased female dietary stress associated with gestation and infant care may have also played a significant role in influencing guenon positional behavior.

Guatier-Hion (1980) reported that for several species of guenon, dietary variation between males and females is greatest when females are either pregnant or lactating. Gautier-Hion (1980) found that pregnant or lactating female guenons meet increased protein demands by shifting their diet from fruit to leaves and live prey. Of the two groups composing the Central Guenons at BFMS, every adult female
except one in the smaller of two groups gave birth during the observational period (Figure 8.10). In the larger group, many females had unweened, young offspring. Though they were less frequently startled by approaching humans than were colobus mothers, guenon mothers did carry infants long distances and often across numerous large gaps in arboreal pathways. Coupled with the energetic costs of lactation, the energetic demands of being a female guenon mother might therefore be substantially higher than those of a male.

**Figure 8.10: Female *C. campbelli lowei* and offspring.** Infants regularly traveled with mothers as the groups moved back and forth between the village and the western portion of their range. Young offspring would often take advantage of the short resting periods between movements by nursing.

It is possible that female guenons meet greater dietary needs by more frequently employing those postures that facilitate the acquisition of their preferred
food resources. McGraw (1998b) argued that high frequencies of Stand postures exhibited by guenons were associated with their diet. Since fruit and insects are food sources typically associated with a high degree of feeding competition (Garber, 1987; Oates, 1987), Stand postures might be employed by guenons as a means to rapidly transition into contextually appropriate locomotor modes once food is identified in order to outcompete conspecifics (McGraw, 1998b). Both Cords (1986) and Gautier-Hion (1980) found that guenon females in several species increased their consumption of insects and decreased their consumption of fruit during lactation. If this was true for *C. campbelli lowei* as well, Stand postures might have been particularly beneficial to females attempting to identify and then move rapidly to capture cryptic and mobile insect prey. If female guenons were under greater dietary stress than male guenons, therefore, they might have mitigated that stress by employing more foraging-associated postures (i.e., Stands) than did males. Female Central Guenons did, in fact, engage in Stand postures nearly 6% more frequently than did males.

If Stand postures were being adopted by female guenons at a higher frequency than they were in males primarily to enhance their ability to compete over food, I predicted that females would engage in locomotor behaviors that would rapidly allow them to move towards those food resources. At BFMS, the ability to rapidly move toward feeding locations would also enhance the ability of *C. campbelli lowei* to outcompete both fellow group members as well as members of adjacent groups in acquiring scavenged food from the village and food offered by visiting
tourists. While male and female guenons engaged in Quadrupedalism more than twice as often as any other locomotor behaviors, this locomotor behavior was often used during long-distance travel across the guenon’s home range. I predicted the locomotor behaviors most likely to be used during foraging would be Leap and Horizontal Climb. Both allow for direct travel between discontinous supports where guenons can aquire either fruit/seeds located near the periphery of the tree crown or insect eggs attached to the underside of leaves. Female guenons did engage in Horizontal Climb at nearly twice the frequency that males engaged in Horizontal Climb (19.3% vs. 9.4%). Leap frequencies, however, differed only slightly between the sexes.

Different Social Roles Drive Male/Female Differences in Positional Behavior

In addition to the influence of body size and/or dietary stress, differing social roles have been used to explain sex-based differences in primate positional behavior (Chatani, 2003). Among some primate species, males may play a greater role in territorial vigilance than do females and this increased vigilance has been suggested as a possible explanation for alpha male tolerance of less dominant males (van Schaik and van Noordwijk, 1989). Males, unburdened by infant care, may be able to devote more of their time to social behaviors like vigilance (van Schaik and van Noordwijk, 1989) or other social activities like being groomed or displaying dominance (Chatani, 2003). Time devoted to high levels of vigilance might come at the cost of not being able to efficiently engage in other activities like feeding. For
example, Cords (1990) suggested that feeding bouts may be prolonged as individuals attempt to balance vigilance activity and scanning for food resources. Predation avoidance is often proposed as the primary benefit of effective vigilance (van Schaik and van Noordwijk, 1989; Cords, 1990). Though predation risks seem fairly low at BFMS (see Chapter 2), vigilance may play many other important roles such as detecting potential competitors within groups, identifying movement of extra-group individuals (e.g., members of invading groups, extra-group males), and reacting to human encroachment (e.g., cars, tourists).

Male and female *C. vellerosus* differed substantially in their social roles. Sicotte and Macintosh (2004) reported that male *C. vellerosus* initiate most aggressive intergroup encounters at BFMS, often displacing males and females of neighboring groups from shared feeding sites, and were the most active participants in these conflicts. During this study, *C. vellerosus* males were actively involved in territorial defense, often chasing away extra-group individuals, patrolling the periphery of the group’s range, and aggressively displaying. In groups composed of multiple males, like *C. vellerosus*, less dominant males are often displaced from the center of the group and can provide extra vigilance along the periphery (van Schaik and van Noordwijk, 1989). While colobus males of all ranks often worked together to defend their group’s range from external threat, conflict between adult males within groups was quite common.

The significant role that male colobus play in defending their territory and displaying their dominance were predicted to influence both their postural and
locomotor behavior. I predicted that if male colobus were more vigilant than female colobus and if this behavior drove postural differences between the sexes, males would have engaged in *Sit* postures more frequently than females and *Recline* postures less frequently. *Sit* postures may have facilitated a male’s ability to freely turn his head and scan his entire range of vision. More importantly, since colobus rarely *Stand*, *Sit* was the alternative posture that best allowed males to react quickly to any perceived threat and easily graded into a variety of locomotor behaviors including the leaping displays and bounding common among black-and-white colobus males (Mittermeier and Fleagle, 1976; Oates and Trocco, 1983). As predicted, Wawa Colobus males did, in fact, *Sit* more and *Recline* less frequently than did females.

If the ability to identify and quickly respond to potential threats drove postural differences between males and females, we might expect it to have also influenced male colobus locomotion. The aggressive nature of inter and intragroup conflicts suggests that speed is an important component to chasing off potential threats (Sicotte and Macintosh, 2004). This was evident in the conflict between adult males within the Wawa Colobus group. The male dominance hierarchy was unclear throughout much of the study as the two adult Wawa males spent a substantial proportion of the day rapidly chasing one another away from the central position in the group. Similarly, when extragroup individuals were perceived as a potential threat, resident male colobus responded with direct, quick pursuits. If direct paths were available, I predicted that males would engage in *Quadrupedalism*.
which might provide the least risky and most energy efficient means to cross their range. Black-and-white colobus have been shown to prefer horizontal travel pathways when traveling and minimize vertical movement (e.g., moving downward to access large boughs upon which they can move quadrupedally) through the use of short leaps (Gebo and Chapman, 1995). When male colobus at BFMS encountered breaks in the canopy, I predicted that they would minimize travel time and straighten arboreal pathways by choosing to Leap across those gaps rather than slowly climbing through thin branches along the periphery of tree crowns. Male colobus did Leap >10% more frequently than did females and engaged in Horizontal Climb less frequently, however females engaged in Quadrupedalism at a slightly higher frequency (~3%).

In contrast to those of C. vellerosus, male and female social roles for C. campbelli lowei were considerably different. Male guenons used loud calls in conjunction with other non-vocal forms of communication (e.g., head-bob threats, arm lifts) to monitor territory, to advertise their quality, and to dissuade potential threats to their range (Zuberbuhler, 2002). Males, however, rarely involved themselves physically in intergroup conflict. Philopatric female guenons played an aggressive role in intergroup conflicts by grouping together, initiating chases against potential threats, and even aggressively attacking and killing conspecific threats (Cords, 1987; McGraw, 2002). During these conflicts, females of each group would gather together in adjacent areas of vegetation and vocalize until one of the two groups initiated a chase. When successful, these chases usually pushed one
group out of their initial tree or bush, only to regroup and respond in kind with a subsequent chase. Since female guenons spent the majority of their time in the forest understory (50% of all observations—Chapter 5), there were few long, horizontal supports that could facilitate direct, long-distance Quadrupedalism. Therefore, I predicted that if social roles drove locomotor contrasts between male and female Central Guenons, female guenons would exhibit increased frequencies of Leap and Horizontal Climb when compared to males. These locomotor behaviors might have provided the most direct means of chasing potential threats and moving across one’s range along flexible, thin understory supports. While rates of Horizontal Climb were higher for female Central Guenons than male Central Guenons (19.3% vs. 9.3%), rates of Leap were similar between the sexes.

Positional Behavior: The Multivariate Problem

Identifying the relative contributions that differences in body size, energetic requirements and social roles may play in producing the sex-based intraspecific differences in positional behavior identified in this study is challenging. This is due to the fact that many factors have likely influenced the positional behavior of both species. It is possible, for instance, that postural and locomotor profiles for female colobus were constrained by their increased energetic demands at the same time that postural and locomotor profiles of male colobus were constrained by their social responsibilities. I argue that to understand the intraspecific differences identified here, one needs to consider all of these three factors (i.e., body size, social
roles, and dietary stress) together in the context of the species under study. I suggest possible explanations for these results for each primate species below.

I recorded higher rates of Sit for colobus males and higher rates of Recline for colobus females. These results fit predictions for both the dietary stress and body size hypotheses. I also recorded higher rates of Leap for male colobus than female colobus but lower rates of Horizontal Climb and Quadrupedalism. I had predicted higher Leap frequencies for males under the social roles hypothesis and higher Horizontal Climb frequencies for females under the dietary stress and body size hypotheses. The ambiguity of these results suggest that several factors are interacting to produce the postural and locomotor differences observed for male and female colobus. When all male/female observations are compared by their forest strata location for Wawa Colobus, males were observed slightly more frequently in the upper canopy (20m+) while females were found more frequently in the lower canopy (10m–15m) and the understory (≤5m) (Table 8.13; Figure 8.11). The tendency for male colobus to be found higher in the upper canopy may shed light on sex-based intraspecific differences in positional behavior observed for Wawa Colobus.

<table>
<thead>
<tr>
<th>Wawa Colobus</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m–15m</th>
<th>20m+</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>2.6%</td>
<td>20.0%</td>
<td>29.7%</td>
<td>47.7%</td>
<td>4091</td>
</tr>
<tr>
<td>Male</td>
<td>2.3%</td>
<td>18.8%</td>
<td>26.5%</td>
<td>52.4%</td>
<td>1404</td>
</tr>
</tbody>
</table>

Table 8.13: Forest Strata Profiles for Male and Female Wawa Colobus.
The dense understory at BFMS largely obscured long-distance observation. If male colobus were placing themselves higher in the forest canopy more frequently than females, it may have been because of the observational advantages such heights afforded them. Higher frequencies of Sit postures may have facilitated such observation (e.g., easily rotate head to scan range) and allowed male colobus to quickly respond to perceived threats (e.g., transition more quickly into locomotion than might be possible in the Recline posture). When traveling, males might have opted for more direct travel paths, incorporating Leaps whenever they served to straighten their arboreal pathways. By travelling as directly as possible, male colobus could move rapidly between resting locations where they could Sit and observe surrounding groups and to quickly respond to competitors.
Female colobus played a less active role in monitoring and defending territory. Burdened by greater dietary stress, female colobus may have frequently moved and fed in the periphery of tree crowns where many leaf resources were located. This may have been facilitated by the female’s smaller body size, allowing them to exploit some resources that males could not. While moving between these feeding locations, females might have opted for less direct and more exploratory travel routes. This seemingly slower movement would have been facilitated by higher frequencies of *Horizontal Climb* and might have offered females the opportunity to forage frequently along the way. It is possible, then, that body size offered female colobus the opportunity to meet potentially higher dietary demands while feeding in the same strata as males.

If social responsibilities, body size and dietary stress all played a role in patterning colobus positional behavior profiles, could the same have been true for guenons? Despite very different social patterns and forest strata preferences, guenon males, like colobus males, were observed in upper canopy more frequently than guenon females (Table 8.14, Figure 8.12). Male guenons were also found on the ground more frequently than female guenons. The most striking contrast between the species was found in the forest understory. While 50% of all observations of female Central Guenons occurred when they were in the forest understory, only one-third of all observations of male guenons occurred when they were in the same forest stratum. Male guenons engaged in *Sit* postures approximately 5% more frequently than did females and *Stand* postures approximately 5% less frequently.
Males also engaged in *Quadrupedalism* approximately 10% more frequently than females and *Horizontal Climb* approximately 10% less frequently. I argue that these differences can be explained in the context of differing social roles, increased female dietary stress, and differences in body size.

<table>
<thead>
<tr>
<th>Central Guenons</th>
<th>Ground</th>
<th>≤5m</th>
<th>10m–15m</th>
<th>20m+</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>2.5%</td>
<td>50.0%</td>
<td>28.3%</td>
<td>19.2%</td>
<td>4612</td>
</tr>
<tr>
<td>Male</td>
<td>10.1%</td>
<td>32.8%</td>
<td>30.4%</td>
<td>26.7%</td>
<td>771</td>
</tr>
</tbody>
</table>

**Table 8.14: Forest Strata Profiles for Male and Female Central Guenons.**

Just as male colobus routinely monitored their territory, male guenons regularly traveled high in the forest canopy to observe the movement patterns of neighboring groups. The coordinated movements between neighboring groups was
critical in acquiring highly valued food items at BFMS (e.g., products of frequently used feeding trees, discarded foods along the village edge, foods offered by visiting tourist groups). Particularly for the smaller of the two Central Guenon groups, arriving late at a feeding site might result in a group having to fight to gain access to that site, or, if they are unwilling to engage in a fight, being displaced entirely from that site and having to wait for the adjacent group to move away. This resulted in highly coordinated movement patterns between neighboring groups. When one group began travel toward or away from the village, the adjacent group often did the same. In these coordinated movements, males would often serve as “lookouts,” patrolling the periphery of their territory and signalling for potential threats through vocalizations. If they chose to do so, females might then abandon their continuous foraging in the understory, quickly move toward the male, and engage in any fight directly. This pattern of male vigilance (i.e., resting high in the canopy and observing potential male threats) is common in several other guenon species and has been attributed to their single-male group structure (Gautier-Hion, 1980).

Gautier-Hion (1980) argued that many behavioral contrasts between male and female guenons derive from two factors: 1) where those behaviors tend to occur and 2) differences in foraging strategies between the sexes. I argue that sex-based postural differences for guenons at BFMS are best explained through the combined influence of increased dietary demands for females, exacerbated by the additional energy they must devote to intergroup conflict, and the social role played by males in territory monitoring. Increased frequencies of Sit and Recline postures
may seem to run counter to the notion that male guenons are defending their territory. Unlike colobus males, however, guenon males rarely engaged directly in intergroup conflict. Instead, males played an active role in identifying threats and calling attention to them while relying on females to discourage or defend against those threats through intergroup conflict. I argue that female guenons engaged in *Stand* postures more frequently than males for two reasons. First, during periods of intergroup conflict, *Stand* postures might quickly transition into *Leap, Horizontal Climb*, or some other locomotor behavior needed to initiate or react to chases. Second, if females were under greater dietary stress and responded to that stress by increasing consumption of insect prey (Gautier-Hion, 1980; Cords, 1986), *Stand* postures might facilitate rapid movement to acquire high competition, mobile food resources.

Additionally, *Horizontal Climb* behaviors might facilitate movement through the flexible, thin supports found in the dense forest understory. Whether involved in intergroup conflicts or continuous foraging travels, smaller-bodied female guenons might benefit from the flexibility of being able to travel along thinner supports that the male’s larger body size might constrain them from using. In contrast, males often moved around the periphery of their home range and it was not uncommon for males to move far away from the group for long periods of the day. Males might move repeatedly from one end of their range to the other while watching for potential threats or the movement of adjacent groups.
Primate leaping generates huge take-off forces (Demes et al., 1995). The high risks and energetic costs associated with leaping may cause primates to pattern movement in ways that minimize their exposure to canopy gaps (Cannon and Leighton, 1994). In order to conserve energy during their travels, male guenons likely engaged in Quadrupedalism, their preferred locomotor behavior, whenever possible. The large boughs radiating out from the trunks of trees in the upper canopy also probably provided more opportunities for direct Quadrupedal locomotion between distant points in their range than females had in the understory. This pattern of direct, long-distance male travel may also explain the more frequent use of terrestrial supports by males than females. For example, males frequently made use of the existing trail system in order to quickly move across their range (Figure 8.13). McGraw (1996b) similarly observed that C. campbelli campbelli in the Tai Forest frequently drops to the ground for long-distance travel.
Figure 8.13: Trail Use by Male *C. campbelli lowei*. This photo depicts the alpha male of one of the Central Guenon groups traveling along one of the main East-West trails at BFMS. Males frequently used these trails or traveled along the long boughs found in the upper canopy while patrolling their home range.

While both species exhibited sex-based differences in positional behavior, such differences must, of course, be considered in their proper context. First, the sample size for observed male positional behaviors, particularly for guenons, is quite low and may be somewhat biased by the opportunities in which males were observable. It may be, for instance, that as male guenons moved away from their groups they adopted postures or locomotor behaviors to a different degree than they did when they were with their groups. When near their group, male guenons may have felt less threatened by extra-group individuals and exhibited less urgent
forms of positional behavior such as slow Quadrupedalism, Sits, and Reclines. While patrolling further away from their group, males may have felt less secure and engaged in postural and locomotor behaviors that would facilitate rapid retreats (e.g., Stands, Leaps) if threatened. The research method (i.e., focal samples rotating between adjacent animals) used in this study may not have captured these more elusive male behaviors.

Given this caveat and even with the statistically significant differences in postural and locomotor profiles identified in this chapter, there were clear similarities between males and females for each species. In previous chapters, I argued that the conservative nature of positional behavior is evident in the consistent overall positional behavior patterns between forest types. This trend appears to be maintained between the sexes as well. In Table 8.15, I list the different postures and locomotor behaviors used by male and female colobus and guenons ranked by their frequency of use. Despite differences in the frequency of certain postures, colobus males and females both Sit much more often than they Recline. Guenon males and females both adopt Sit postures the most, followed by Stand postures, and finally Recline postures. Similarly, male and female colobus rely most heavily on Leaping and Quadrupedalism (though males Leap far more than they move via Quadrupedalism) followed by Horizontal Climb and Vertical Climb. For guenons, Quadrupedalism was the dominant locomotor mode followed by Horizontal Climb and Leap with lower frequencies of Vertical Climb.
### Table 8.15: Ranked Male and Female Postures and Locomotor Behaviors

<table>
<thead>
<tr>
<th>Wawa Colobus Postures</th>
<th>Central Guenon Postures</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Sit</td>
<td>1. Sit</td>
</tr>
<tr>
<td>2. Recline</td>
<td>2. Stand</td>
</tr>
<tr>
<td>3. Other</td>
<td>3. Recline</td>
</tr>
<tr>
<td></td>
<td>4. Cling</td>
</tr>
<tr>
<td></td>
<td>5. Other</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Wawa Colobus Locomotion</th>
<th>Central Guenon Locomotion</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Leap or Quadrupedalism*</td>
<td>1. Quadrupedalism</td>
</tr>
<tr>
<td>2. Quadrupedalism of Leap*</td>
<td>2. Leap</td>
</tr>
<tr>
<td>3. Horizontal Climb</td>
<td>3. Horizontal Climb</td>
</tr>
<tr>
<td>5. Drop</td>
<td>5. Drop</td>
</tr>
</tbody>
</table>

This table lists the postures and locomotor behaviors displayed by both male and female Wawa Colobus and male and female Central Guenons ranked by the frequency at which each was observed. *Female colobus engaged in Quadrupedalism and Leap at very similar frequencies while male colobus engaged in Leap far more frequently than Quadrupedalism.

Therefore, the question of whether males and females utilize different patterns of positional behavior is one of resolution or scale. This study provides evidence that males and females of the same species can exhibit significantly different positional behavior profiles and that these differences can be explained by differing dietary, social, and body size constraints. Teasing out one factor to explain those differences (e.g., energetic costs of locational, role in intergroup conflict) is unlikely to satisfactorily explain any observed differences because of the multivariate nature involved in a primate’s decision to select one posture or locomotor strategy over another. These differences are potentially ecologically significant and help to explain existing behavioral variation in these primate species. However, the commonalities between male and female patterns of postural and
locomotor behavior (i.e., the likelihood that they will use one behavior over another) are clear and support the notion that a primate’s evolutionary history strongly constrains its positional behavior.

**Conclusion**

In this chapter, I tested for statistically significant intraspecific sex differences in the posture and locomotion of *C. vellerosus* and *C. campbelli lowei*. The results of these tests are summarized below:

1. The overall posture and locomotor profiles of male and female colobus and guenons in unlogged, western forest at BFMS differed significantly. Due to small sample sizes, these profiles were not tested for each of the maintenance activities recorded in this study. However, locomotor differences during Non-Social Locomotion likely drove intraspecific locomotor contrasts and postural differences during Rest likely drove intraspecific postural contrasts.

2. Male colobus exhibited higher frequencies of *Sit* and lower frequencies of *Recline* than did female colobus. Male colobus engaged in *Quadrupedalism* and *Horizontal Climb* less frequently and *Leap* more frequently than did females.

3. Male guenons exhibited higher frequencies of *Sit* and *Recline* but lower frequencies of *Stand* than did female guenons. Male guenons engaged in
Quadrupedalism more frequently and Horizontal Climb less frequently than did females.

4. Male colobus were found more frequently in the upper canopy. Sit may offer males the most efficient means to identify and quickly respond to potential threats. Males may also have shortened their arboreal pathways by engaging in Leap rather than less risky Quadrupedalism or slower Horizontal Climb behaviors because of their role in chasing potential competitors and their travel in the upper canopy. Females may have followed less direct pathways and used Horizontal Climb more frequently not to feed of resources in lower forest strata than males but rather to exploit leaf resources found in in the periphery of tree crowns.

5. Male guenons were also found in the upper canopy at higher frequency than were females. They may have engaged in Sit and Recline postures for frequently as they attempted to identify potential threats and warn other group members through loud vocalizations. Females may have adopted Stand postures more frequently because they facilitated both rapid responses to potential threats but also the acquistion of mobile and/or highly competitive food items. Females were frequently found in the understory where Horizontal Climb likely provided an efficient means of moving between the many thin, discontinous supports found there. Higher rates of
Quadrupedalism for males may have been associated with their role in patrolling the periphery of their home range.

Just as habitat appears to influence some elements of positional behavior for female colobus and guenons at BFMS, biological and behavioral differences between males and females also can be tied to intraspecific positional behavior variation. While we might expect this to be the case given the different roles that males and females play in the day-to-day activities of primate groups, species-specific distinctions between guenon and colobus positional behavior profiles is evident. In other words, it remains clear that, no matter the sex, a colobus is a colobus in terms of its preferred locomotor and postural modes (i.e., frequent leaper and sitter).
Chapter 9: Project Summary and Significance

Project Overview

In this project, I tested the degree to which primate postural and locomotor behaviors, usually referred to collectively as positional behavior (Prost, 1965), are conserved within primate species. Through field observations of the ursine colobus (C. vellerosus) and Lowe’s monkey (C. campbelli lowei) at Boabeng-Fiema Monkey Sanctuary, Ghana, I collected instantaneous focal data on both species and conducted intraspecific behavioral comparisons by both habitat and sex. The goals of this study included documenting the positional behavior profiles of both species, examining the degree to which habitat disturbance affected the positional behavior of both species, and testing whether males and females differed in positional behavior. If positional behavior did prove to be variable for either species, such differences might have important implications for form-function associations used by functional morphologists in reconstructing the behavior of fossil species. Thus, the broader significance of this project derives from the four following questions:
**Question 1: What are the positional behavior profiles for C. vellerosus and C. campbelli lowei at BFMS?**

Throughout the preceding chapters, I have documented the support usage and positional behavior profiles for two West African monkey species. These profiles will contribute to a growing number of positional behavior studies dedicated to documenting the range of locomotor and postural variation found within the Primate Order. As Fleagle (1979) noted, developing associations between morphological and behavioral variation in living species helps us understand modern primate variation and serves as one of the few tools we have for recreating the lifeways of past species. This requires quantitative and wide-ranging studies of positional behavior and anatomy for extant primate species. This study documents quantitative positional behavior data on *C. vellerosus* and *C. campbelli lowei*.

Given the intraspecific differences in positional behavior identified in this study, colobus and guenons living in unlogged, western forest at BFMS likely serve as better representatives of species-typical positional behavior than do those in more disturbed southern forest. Female positional behavior was more frequently sampled for both species than was male positional behavior and as a result is less likely to be subject to observational bias. Tables 9.1 and 9.2 summarize the positional profiles for female colobus and guenons found in the least disturbed habitat at BFMS. These results are extrapolated from data presented in chapters 5–7.
<table>
<thead>
<tr>
<th></th>
<th>Summarized Behavioral Patterns and Preferences</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat Usage</strong></td>
<td>- Preferred upper canopy, followed by lower canopy and then understory</td>
</tr>
<tr>
<td></td>
<td>- Relied predominantly on horizontal supports with a preference for Boughs over Branches</td>
</tr>
<tr>
<td><strong>Posture</strong></td>
<td>- <em>Sit</em> was the dominant posture followed by <em>Recline</em></td>
</tr>
<tr>
<td></td>
<td>- Alternate postures, particularly <em>Stand</em>, were rare</td>
</tr>
<tr>
<td><strong>Locomotion</strong></td>
<td>- <em>Quadrupedalism</em> and <em>Leap</em> were the dominant locomotor behaviors</td>
</tr>
<tr>
<td></td>
<td>- <em>Horizontal Climb</em> and <em>Vertical Climb</em> were employed less frequently</td>
</tr>
<tr>
<td></td>
<td>- Drops and <em>Other</em> locomotor modes were rarely observed</td>
</tr>
</tbody>
</table>

**Table 9.1: C. vellerosus Habitat Usage and Positional Behavior.** This table summarizes data displayed in chapters 5–7 regarding observed habitat usage and positional behavior patterns for female colobus found in unlogged western forest at BFMS.

<table>
<thead>
<tr>
<th></th>
<th>Summarized Behavioral Patterns and Preferences</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat Usage</strong></td>
<td>- Preferred forest understory with minimal use of the upper canopy or ground</td>
</tr>
<tr>
<td></td>
<td>- Relied predominantly on horizontal supports with a slight preference for Branches over Boughs</td>
</tr>
<tr>
<td><strong>Posture</strong></td>
<td>- <em>Sit</em> was the dominant posture</td>
</tr>
<tr>
<td></td>
<td>- <em>Stand</em> postures were more frequently employed than <em>Recline</em> postures</td>
</tr>
<tr>
<td></td>
<td>- <em>Cling</em> postures were rarely observed</td>
</tr>
<tr>
<td><strong>Locomotion</strong></td>
<td>- <em>Quadrupedalism</em> was the dominant locomotor mode</td>
</tr>
<tr>
<td></td>
<td>- <em>Leap</em> and <em>Horizontal Climb</em> were less frequently employed alternatives</td>
</tr>
<tr>
<td></td>
<td>- <em>Vertical Climb</em> were less commonly employed</td>
</tr>
<tr>
<td></td>
<td>- Drops and <em>Other</em> postures were rarely observed</td>
</tr>
</tbody>
</table>

**Table 9.2: C. campbelli lowei Habitat Usage and Positional Behavior.** This table summarizes data displayed in chapters 5–7 regarding observed habitat usage and positional behavior patterns for female guenons found in unlogged western forest at BFMS.

Female *C. vellerosus* in the least disturbed forest at BFMS preferred the upper canopy. While the monkeys used all canopy levels and support sizes to an extent, even coming to the ground on occasion, the large, horizontal supports found in the upper canopy were their preferred substrate. Female colobus engaged in *Sit* postures far more frequently than *Recline* postures and rarely engaged in *Stand* postures. *Sit* postures are not unusual for highly folivorous primates that feed in long bouts from a single bunched food resource (Oates, 1987). While traveling,
females engaged in Quadrupedalism and Leap behaviors at nearly equal frequencies and more frequently than they engaged in any other locomotor behaviors. This is likely tied to their preference for large, horizontal, upper canopy supports. These supports often radiated outward from the central trunk in such a way that they afforded direct paths easily navigated through Quadrupedalism from the center of the tree to the periphery. As has been observed for other black-and-white colobus (Morbeck, 1977; Gebo and Chapman, 1995), as agile leapers, female colobus preferred Leaps over Horizontal Climbs as a means of crossing between supports.

Female C. campbelli lowei preferred the forest understory. Terrestrial food resources likely played a large role in drawing guenons to this stratum. In western forest at BFMS, guenons frequently fed just above the ground in the forest understory (Figure 9.1). Guenons regularly (usually twice daily) raided village storehouses, meal preparation areas, and discarded refuse heaps for food items. Tourists visiting the site and local villagers traveling between the village and nearby farms also frequently fed the guenons. These resources were located on or near the ground and the behavior of the guenons suggested that these resources were highly desirable. Guenons carefully monitored neighboring groups, moved in tandem towards areas of their ranges with access to the village, and closely defended their control over their portion of the village edge. In other disturbed forest fragments, monkeys have been shown to increase their use of the forest understory when they are likely to acquire foods discarded on the ground by humans. For example, Siemers (2000) found that Cebus apella increased their time in the forest understory
for all activities (e.g., resting, foraging for naturally occurring foods, travel) during times of the year when discarded human food was commonly consumed. Interspecific comparisons between guenons have shown that foraging rates for some food types and forest strata (e.g., fruits in upper canopy) are more closely associated than for others (insects) (Tashiro, 2006). Without dietary data, it is difficult to say what foods *C. campbelli lowei* at BFMS ate, however, *C. campbelli lowei* did feed frequently on discarded human foods and actively approached visitors to the site in anticipation of being fed. As guenons followed and maintained proximity to terrestrial food sources, the architectural nature of the forest understory may have influenced their positional behavior in ways that are not found at less tourist-driven primate habitats. I argue that common characteristics of supports regularly used by guenons in the understory affected their postural profiles.
Figure 9.1: Understory Feeding in *C. campbelli lowei*. The photo on the left shows a guenon feeding on a captured insect. The photo on the right shows several guenons congregating on the branches of a dead tree and feeding on human refuse scavenged from a garbage dump below (not pictured).

Saplings and the small, low-hanging branches of mid-sized trees dominated the forest understory in unlogged western forest. This architectural arrangement likely accounted for female guenon’s slight preference of branches over boughs. Female guenons preferred to *Sit* while resting but, unlike colobus, rarely reclined. Like other closely related guenons that rely on highly competitive fruit and insect resources (Buzzard, 2006), guenons at BFMS may have engaged in *Stand* postures in order to facilitate rapid acquisition of prey (McGraw, 1998b) and/or to distribute their body mass across thin, flexible understory supports (see chapter 6). *Stand* postures grade easily into different locomotor behaviors allowing rapid locomotor
responses to environmental stimuli—e.g., threats, desired food items, etc. (Rose, 1974, McGraw 1998b). The most commonly used locomotor behavior for female guenons was Quadrupedalism though Leaps and Horizontal Climbs were used at lower frequencies and provided alternate modes of locomotion when Quadrupedalism was untenable (e.g., along flexible supports in the forest understory or near the periphery of tree crowns, crossing gaps between tree crowns).

**Question 2: Do differences in forest structure between habitats result in significant changes in positional behavior repertoire?**

I addressed the question of positional behavior variation by comparing females from groups of *C. vellerosus* and *C. campbelli lowei* inhabiting portions of the BFMS forest fragment that were architecturally distinct in several ways. More disturbed southern forest differed most dramatically from less disturbed western forest in reduced canopy density and the architectural nature of its densely tangled forest understory. The results of intraspecific comparisons for each species are listed in Table 9.3.
I identified a number of statistically significant differences between colobus and guenon females inhabiting southern and western forest. Female members of each species differed significantly in the frequency at which they used different forest strata and supports of differing characteristics. The difference between forest types was consistent in that both species tended to use lower forest strata in more disturbed southern forest and the thinner supports that dominate these strata at higher frequency. Given these contrasts in habitat use, I anticipated that guenons and colobus in disturbed southern forest might also differ from those in western forest in their postural and locomotor profiles. Both species exhibited intraspecific variation in their postural profiles, particularly postures adopted during Rest. Only guenons differed in their locomotor profiles, particularly locomotor behaviors adopted during Non-Social Locomotion.
In chapters 6 and 7, I argued that intraspecific variation in posture (for colobus and guenons) and locomotion (for guenons) derived from the combined influence of diet, body size, and forest architecture. This argument is outlined in Figure 9.2. For both species, I argued that the upper canopy in disturbed southern forest offered few direct arboreal pathways and those that remained were not evenly distributed across the respective home ranges of the primate species found there. Alternative pathways in the lower canopy and understory likely provided a more direct travel route across substantial portions the southern forest. For colobus, increased use of the forest understory and lower canopy led to increased use of smaller supports (both Twigs and Branches) near alternative leaf resources located in the periphery of smaller tree crowns (lower canopy) or in the tangled vegetation found near the forest floor. In contrast, guenons in southern forest used the thin supports found in the forest understory more frequently, likely foraging for insect and alternate, low-hanging fruit resources. For both species, I argued this led to adjustments in their postural profiles. Colobus engaged in *Sit* postures more frequently because these postures were more stable and allowed them to distribute their weight across multiple supports. Guenons engaged in *Stand* postures more frequently because in the heaped masses of vegetation, *Stand* may have been more stable and may have better facilitated rapid acquisition of highly competitive food resources. Guenons further adjusted their locomotor profiles by incorporating higher frequencies of *Leap* and *Horizontal Climb*, both behaviors well-suited for the undulating, dense, and entangled southern forest understory.
Figure 9.2: The Affects of Anthropogenic Disturbance on *C. vellerosus* and *C. campbelli lowei* Positional Behavior.
This intraspecific variation is significant for two primary reasons. First, this study provides evidence that the behavioral plasticity often ascribed to other behavioral traits for members of the Primate Order can also be found, albeit to a limited degree, in primate positional behavior. Second, while changes in positional behavior are rarely considered in the context of anthropogenic disturbance, this study shows that man-made changes in forest structure can and do influence a primate's locomotor and postural decisions.

**Question 3: Do differences in the social roles and the biology of male and female monkeys at BFMS produce intraspecific variation in positional behavior?**

Though field studies have rarely shown significant intersexual differences in positional behavior, sexual dimorphism, contrasting social responsibilities, and differences in dietary stress have all been considered as causal agents for why male and female positional behavior might vary (see Garber, 2007 for a review). Both *C. vellerosus* and *C. campbelli lowei* are sexually dimorphic species (Delson et al., 2000) and males and females in these species differ dramatically in their respective contributions to territorial defense, extragroup vigilance, and infant care (see chapter 8). Given these behavioral, physiological, and morphological contrasts, I compared the postural and locomotor profiles for male and female colobus and guenons in unlogged, western forest at BFMS. I did identify significant differences in postural and locomotor profiles between males and females in both species. The greatest sex-based postural and locomotor differences are summarized in Table 9.4.
Table 9.4: Sex-Based Postural and Locomotor Differences for Colobus and Guenon.
This table summarizes some of the largest frequency differences between the overall postural and locomotor profiles of male and female *C. vellerosus* and *C. campbelli lowei* in unlogged western forest at BFMS.

<table>
<thead>
<tr>
<th></th>
<th>Posture</th>
<th>Locomotion</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. vellerosus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>• Higher Recline Frequency</td>
<td>• Higher Horizontal Climb Frequency</td>
</tr>
<tr>
<td></td>
<td></td>
<td>• Higher Quadrupedalism Frequency</td>
</tr>
<tr>
<td>Male</td>
<td>• Higher Sit Frequency</td>
<td>• Higher Leap Frequency</td>
</tr>
<tr>
<td><em>C. campbelli lowei</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>• Higher Stand Frequencies</td>
<td>• Higher Horizontal Climb Frequency</td>
</tr>
<tr>
<td>Male</td>
<td>• Higher Sit Frequency</td>
<td>• Higher Leap Frequency</td>
</tr>
<tr>
<td></td>
<td>• Higher Recline Frequency</td>
<td>• Higher Quadrupedalism Frequency</td>
</tr>
</tbody>
</table>

Male colobus and male guenons used the upper canopy more frequently than did females, which I argued was tied to their more vigilant social role. Once a male colobus observed a potential threat, they actively engaged those threats during both inter and intragroup conflicts. Increased frequencies of *Sit* postures may have enabled male colobus to better monitor and quickly respond to those threats. The increased frequency of *Leaps* for males suggests that they were opting to shorten arboreal pathways. Whether this facilitated territorial monitoring or reflected less of a concern for energy expenditure is unclear. In contrast, guenon males rarely engaged physically in conflicts. The increased frequencies of *Sit* postures and *Quadrupedalism* for male guenons likely reflected their tendency to move back and forth across their home range and sit high in the canopy monitoring the movement of surrounding groups. The smaller body size of females may have allowed them to more effectively forage and travel in areas characterized by a high proportion of thin, flexible supports. Increased *Horizontal Climb* frequencies might be expected in
these areas for both species. For colobus females, traveling in the upper and lower canopy, smaller body size may have allowed them to engage in Quadrupedalism along a larger proportion of available supports than could male colobus, resulting in their higher Quadrupedalism frequency. For female guenons, a more active role in intergroup conflicts, often involving chases through densely entangled forest understory, may further have encouraged sex-based intraspecific locomotor variation in this species.

**Question 4: Do the sex-based and habitat-based differences in positional behavior identified in this study bring into question form-function relationships essential to reconstructing the behaviors of fossil primates?**

When a researcher finds fossil remains of extinct primates, there is the hope that living primates sharing similar morphologies can, by analogy, be used to reconstruct at least some aspects of its behavior. In other words, we rely on a certain degree of accuracy in predictive relationships between the morphology and behavior of living specimens to interpret what remains of extinct specimens. If living primates are highly variable in their positional behavior, can we reliably interpret the remains of extinct specimens for which we usually know little about their ecological habitat? Several studies comparing primate positional behavior in different habitats have concluded that a primate’s choice of postures and locomotor modes is largely constrained by its anatomy (Doran and Hunt, 1994; Garber and
Pruetz, 1995; McGraw 1996b). Do the results of this project cast doubt on the conservative nature of primate positional behavior?

These results, while showing that primates can exhibit different postural and locomotor profiles, nevertheless support the consistency of primate positional behavior. For the two activities showing the greatest positional behavior divergence between both habitats and sexes—Rest and Non-Social Locomotion—the differences in the frequencies of particular postures or locomotor behaviors was subtle. For example, colobus did not become climbers when facing more disturbed forest habitat. Instead, they merely favored Quadrupedalism and Leap behaviors to a lesser degree. Similarly, it would be difficult to argue that male guenons were leapers and females were quadrupedalists on the basis of slight sex-specific frequency differences in these behaviors. Moreover, the ranked preferences of particular postural and locomotor behaviors were largely consistent within species, no matter the forest type or sex. For example, male guenons may have engaged in Sit postures more frequently than did females but neither sex sat more frequently than they reclined or stood.

These subtle intraspecific differences, while providing important information regarding the behavioral ecology of living species, pose little threat to established form-function associations. In other words, the consistency in positional behavior demonstrated in this study will cause few to question whether species broadly categorized as exhibiting tendencies towards certain locomotor behaviors (leaping, quadrupedalism, arm-swinging locomotion, etc.) should be reclassified on the basis
of such subtle frequency differences. We might test this idea by comparing species at BFMS to their closest phylogenetic relatives, species with whom they presumably share a great deal of morphological similarity. While there are debates over the monophyletic integrity of their shared clade, *C. campbelli campbelli* is currently believed to be either the sister subspecies or sister species of *C. campbelli lowei* (Grubbs et al., 2003). Using molecular comparisons of mitochondrial base pairs and challenging previous arguments linking *C. vellerosus* phylogenetically to *C. guereza* (Oates and Trocco, 1983), Ting (2008) concluded that *C. vellerosus* is most closely related to *C. polykomos*. If evolutionary history constrains positional behavior, we might expect these closely related species to exhibit similar locomotor and postural profiles.

McGraw (1998a,b) collected positional behavior data on *C. polykomos* and *C. campbelli campbelli* in the Tai Forest, Cote d’ Ivoire. When the postures of closely related colobines and cercopithecines are compared, the similarity between overall postural profiles is evident (Figures 9.3 and 9.4). At both sites, colobus and guenons engaged in *Sit* postures far more frequently than either engaged in *Recline* postures. Guenons also used *Stand* postures at a higher frequency than they did *Recline* postures but a lower frequency than *Sit* postures. That the two guenon groups differed substantially in the frequencies with which they employed *Sit* and *Stand* postures is perhaps unsurprising considering that these two studies were conducted at different times by different researchers with undoubtedly slight
variations in how they recorded different postures. Nevertheless, both species pairs exhibited similar, and in the case of the colobus nearly identical, postural profiles.

**Figure 9.3: Comparison of *C. campbelli campbelli* and *C. campbelli lowei* Postural Behaviors.** This graph compares postural data extracted from McGraw (1998b) for *C. campbelli campbelli* females from the Tai Forest to postural data for *C. campbelli lowei* females from less disturbed western forest at BFMS. McGraw’s (1998b) Sprawl and Lie categories were combined into *Recline* to better match the methods used in this study. The *Cling* category in this study was pooled into the *Other* category as per McGraw (1998b).
Figure 9.4: Comparison of *C. polykomos* and *C. vellerosus* Postural Behaviors. This graph compares postural data extracted from McGraw (1998b) for *C. polykomos* females from the Tai Forest to postural data for *C. vellerosus* females from less disturbed western forest at BFMS. McGraw’s (1998b) Sprawl and Lie categories were combined into Recline to better match the methods used in this study. The Cling category in this study was pooled into the Other category as per McGraw (1998b).

Comparing locomotor profiles between these closely related species was more challenging because of differences between the locomotor definitions used in McGraw (1998a) and those used in this study. Despite this challenge, the general similarity between locomotor profiles for the two guenon species is undeniable (Figure 9.5). Both species engaged in Quadrupedalism far more frequently than either Climb or Leap. Furthermore, females in both species engaged in Climb behaviors at a slightly higher frequency than they did Leap behaviors. Both guenon species could be characterized as preferentially quadrupedal but engaging in climbing and, to a lesser extent, leaping when crossing between discontiguous supports.
Figure 9.5: Comparison of *C. campbelli campbelli* and *C. campbelli lowei* Locomotor Behaviors. This graph compares locomotor data extracted from McGraw (1998a) for *C. campbelli campbelli* females from the Tai Forest to locomotor data on *C. campbelli lowei* females from less disturbed western forest at BFMS. McGraw's (1998a) Quad Walk and Quad Run locomotor categories were combined into *Quadrupedalism* to better match the methods of this study. The present study distinguished between Vertical and *Horizontal Climb*. These were pooled into the Climb category to better match McGraw (1998a). *Drop* was not included in this comparison.

The starkest contrast evident in these comparisons is found in the locomotor profiles of the two colobus species (Figure 9.6). When *Vertical Climb* and *Horizontal Climb* are combined into a single *Climb* category, *C. vellerosus* at BFMS were evenly split on their preference between *Climb*, *Leap*, and *Quadrupedalism*. In contrast, *C. polykomos* at Tai engaged in *Quadrupedalism* far more frequently than they engaged in either *Leap* or *Climb* behaviors.

![Colobus Locomotion: Tai Forest vs. BFMS](image)

Figure 9.6: Comparison of *C. polykomos* and *C. vellerosus* Locomotor Profiles. This graph compares locomotor data extracted from McGraw (1998a) for *C. polykomos* females from the Tai Forest to locomotor data on *C. vellerosus* females from less disturbed western forest at BFMS. McGraw's (1998a) Quad Walk and Quad Run locomotor categories were combined into *Quadrupedalism* to better match the methods of this study. The present study distinguished between Vertical and *Horizontal Climb*. These were pooled into the Climb category to better match McGraw (1998a). *Drop* was not included in this comparison.
Assuming locomotor contrasts between the colobine species are not simply an artifact of different behavioral classification methods (Dagosto and Gebo, 1998), it is possible that ecological differences (e.g., the Tai Forest is a larger, more intact forest) between the sites underly these differences. For example, McGraw (1998a,b) found that approximately 70% of female *C. polykomos* travel time was spent in the upper canopy. Table 9.5 lists the vertical distribution of all locomotor behaviors for female Wawa Colobus at BFMS. While *C. vellerosus* females also preferred the upper canopy for travel, they were found there at a lower frequency than *C. polykomos*. If the Tai Forest offered a wider variety of continuous pathways along long upper canopy boughs than did even the least disturbed upper canopy at BFMS, then it's possible that *C. polykomos* females simply had more opportunities to engage in long-distance *Quadrupedalism*. Should *C. vellerosus* have chosen to restrict itself to Quadrupedalism in the upper canopy, it might have needed to take less direct paths guided by the location of more sparsely distributed large, upper canopy trees.

<table>
<thead>
<tr>
<th></th>
<th>Ground</th>
<th>Understory</th>
<th>Lower Canopy</th>
<th>Upper Canopy</th>
<th>Total Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wawa Colobus Females</td>
<td>5.1%</td>
<td>15.1%</td>
<td>23.8%</td>
<td>56.1%</td>
<td>669</td>
</tr>
</tbody>
</table>

**Table 9.5: Vertical Distribution of Wawa Colobus Locomotor Behaviors.**

With the exception of colobus locomotion, the postures and locomotor profiles exhibited by *C. vellerosus* and *C. campbelli lowei* at BFMS share a marked
similarity to profiles collected for their close phylogenetic relatives. The similarity in overall positional behavior profiles between habitats at BFMS, between sexes at BFMS, and between BFMS and the Tai Forest offer compelling support for the idea that positional behavior is conserved within primate clades.

**Conclusion**

In this study, I have shown that anthropogenic disturbance and sex differences did, in most cases, result in changes in the frequencies of certain positional behaviors for colobus and guenons at BFMS. Several factors that likely contributed to this intraspecific variation include: constraints imposed by morphology and body mass, availability of arboreal pathways between feeding and resting sites, preferred food location, and differences in social roles and responsibilities. I have argued that these differences, while important for understanding subtle variation in the positional behavior of a species in its ecological context, need not cause us to doubt existing form-function associations in living species nor during our interpretations of the fossil record.

Whether the limited plasticity of primate positional behavior exhibited in this study can compensate for the lingering effects of past disturbance at BFMS remains to be seen. Marsh et al. (2003) argued that future efforts to conserve forest fragments that are increasingly critical to endangered primate communities require generating a spirit of cooperation with local communities, providing alternatives and incentives to locals to resist deforestation, and an ability by researchers to consider conservation within the context of the economic, political, and social needs
of surrounding human populations, not just from the perspective of the primates. Ongoing local and international initiatives to protect the primate communities at BFMS (e.g., expanded conservation training by Ghanaian NGOs, increasing awareness of the ties between primate and human health, expansion of the forest through replanting of forest tree species, investment in eco-tourism infrastructure) allow for hope that the coexisting human and primate communities there will persist for the foreseeable future. As Marsh et al. (2003) note, much more research is needed to fully understand the affects or implications of any conservation initiatives and to develop a broader understanding of how to manage forest fragmentation while protecting the health, behavioral and morphological diversity, and self-sufficiency of the primates that live there. In conjunction with the dedication and the on-going work of researchers from the University of Calgary and others, I hope that this study contributes to a greater understanding of the limited plasticity of primate positional behavior generally and the socioecology of C. vellerosus and C. campbelli lowei at BFMS.
References


283


Appendix A: Postural and Locomotor Behaviors

Postural Behaviors Illustrated

Figures A.1–A.4 illustrate examples of the pooled postural categories used to compare groups of *C. vellerosus* and *C. campbelli lowei*. The same categories were used to compare male and female postural profiles for each species. The Other category used in the analysis included those postures that I rarely witnessed. Those few occasions where these behaviors did occur were not captured photographically and are not depicted here. *Stand* and *Cling* were both postural modes observed frequently only for guenons and are depicted below to illustrate guenon comparisons. As stated in chapter 6, these postures were pooled into the Other category for colobus comparisons.
Figure A.1: Cling Postures. This posture was rarely observed for colobus but frequently observed for guenons. Clings associated with vertical or oblique supports were far more common than Clings associated with horizontal supports. The left photo shows a guenon clinging to a branch while foraging and the right shows a guenon grasping the side of a large trunk.

Figure A.2: Recline postures. Reclines included side lies (pictured in left photo), dorsal lies, and sprawls (pictured on right). Guenon Recline postures included side and back lies that appeared similar to that pictured in the left photo but only very rarely sprawled with both hindlimbs straddling a single support.
**Figure A.3: Sit postures.** The left photo depicts a guenon seated on a thin branch reaching upward to forage in leaves out of frame. The right photo depicts a male colobus seated on an oblique branch with his left foot bracing itself against a nearby vertical support. *Sit* postures varied dramatically for both species though they always involved the focal animal's rump and/or thighs supporting the majority of its weight and resting directly against a support.

**Figure A.4: Stand postures.** *Stands* were rarely observed for colobus, likely because their elongated lower limbs make such postures difficult to maintain. The left photo depicts a female guenon standing on a oblique branch. The right shows a male guenon with an orthograde torso supporting his body mass on his hindlimbs assisted by grasped twigs above.
**Locomotor Behaviors Illustrated**

Photos A.5–A.8 illustrate the locomotor modes used to compare *C. vellerosus* and *C. campbelli lowei*. The same categories were used to compare male and female locomotor profiles for each species in unlogged, western forest at BFMS. The *Other* category included those locomotor modes that were rarely witnessed during the study. These were not captured photographically. *Drop* was more commonly witnessed and included as a separate category for analysis but Drops tended to occur very quickly and were not captured photographically.

![Figure A.5: Horizontal Climbs](image)

*Figure A.5: Horizontal Climbs.* The left photo shows a female guenon climbing between flexible terminal branches near the periphery of a tree crown. The right photo shows a female climbing from a large bough into nearby twigs. All *Horizontal Climbs* included any movement between discontiguous supports during which at least one forelimb and one hindlimb was in contact with supports. Consequently, this behavior varied greatly depending in which stratum and on what support it occurred.
Figure A.6: Leaps. *Leap* was a locomotor behavior that included a phase in which no limbs were in contact with a support and was used to cross both large and small canopy gaps. The left photo captures the lower half of a colobus monkey as it leaps between nearby supports. These shorter distance *Leaps* were common in both species but long-distance movement between supports (pictured on the right) occurred frequently when either species crossed trails or areas of cleared/disturbed forest.

Figure A.7: Vertical Climbs. *Vertical Climb* included both vertical ascents like that illustrated by the guenon climbing a thin branch in the left photo and vertical descents like that illustrated by guenons descending down two thin branches in the right photo. *Vertical Climb* differed from *Horizontal Climb* in that it always occurred on a single continuous support or set of supports (e.g., trunks, vertical branches).
Figure A.8: Quadrupedalism. Quadrupedalism included movement along the upper surface of a single continuous support. Quadrupedalism for both guenons and colobus was typically similar to that depicted in the left photo and was characterized by an alternating forelimb/hindlimb quadrupedal gait. Colobus, however, often used a bounding gait (depicted in the right photo) that appeared to blend elements of Quadrupedalism and Leap locomotor behaviors. This behavior was characterized as movement along a single continuous support that included by an aerial phase in which both hands and feet contacted the support in near-unison.