

Positional behavior and habitat use of Peters' Angola black and white colobus monkey
(*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya

THESIS

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Abstract

Positional behavior is the manifestation of both evolutionary and ecological influences. While a number of studies have examined relationships among positional behavior and a variety of ecological variables, the capacity for primates to exhibit intraspecific positional behavior variation in response to changes in forest architecture is not well understood. In order to address this issue, I examined the positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in the Diani Forest of south coastal Kenya from June-August of 2012 to test the degree to which changes in forest structure influence positional behavior. Three troops inhabiting forest patches characterized by varying levels of degradation were observed. Habitat differences were quantified with regard to tree species composition, tree size, and diversity indices. The behavior of adult males and females was sampled instantaneously at 3 minute time intervals.

Overall activity budgets and strata use differed significantly between all troops while support use of one troop was significantly different from that of the others. Overall locomotor and postural behaviors were largely consistent among all habitats. Locomotion was predominantly characterized by arboreal quadrupedal walking and bounding with lesser and relatively equal instances of climbing and leaping. Sitting represented the overwhelming majority of postures and accounted for at least 85% of postural observations for all troops.

I conclude that, because significant differences in activity, strata use, support use, but not positional behavior were realized among structurally distinct sites, *C. a. palliatus* positional behavior is largely constrained by morphology. This allows for more meaningful behavioral reconstructions of fossil primates.

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Fields of Study

Major Field: Anthropology

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Chapter 1: Introduction

The study of primate locomotion and posture (i.e., *positional behavior*) remains a burgeoning research field. Beginning with Prost's (1965) seminal work, researchers have examined positional behavior in order to understand how primates utilize specific locomotor and postural behaviors to negotiate their complex environments.

Understanding why various primate species choose certain positional behaviors or are restricted to certain behaviors based on morphological and/or environmental constraints 1) provides insight into the behavioral ecology of living primates, 2) shapes questions about primate evolutionary adaptations, and 3) aids in reconstructing the behavioral ecology of fossil primates (Fleagle 1979, Fleagle and Meldrum 1988). It is important to stress that positional behavior is the manifestation of both ultimate (i.e., evolutionary) influences and proximate (i.e., ecological) influences (Mayr 1961, 1993, Pounds 1991). In other words, an individual's positional behavior is constrained by the evolution of its particular morphology but is also influenced by its immediate interactions with its environment.

This point may seem obvious now; however, early positional behavior researchers placed primate species into broad locomotor categories (e.g., quadrupeds, brachiators, and semi-brachiators) based largely on presumed musculoskeletal constraints (Napier 1963, Ashton and Oxnard 1964a). These categories were then used to infer aspects of species' evolutionary history and behavior. Evidence for these classifications came

largely from captive observations (Avis 1962), qualitative anecdotes from the field, and/or osteometric analyses (Ashton and Oxnard 1964a, 1964b, Ashton et al. 1965, Oxnard 1967).

Subsequent research revealed that several early conclusions concerning primate positional behavior were contradicted by quantitative field studies (Ripley 1967, Mittermeier and Fleagle 1976, Morbeck 1977). Perhaps the most notable was the classification of colobine monkeys as semi-brachiators—a group characterized by a supposed combination of quadrupedal above-branch behaviors and bimanual suspensory behaviors (Napier 1963). Many aspects of colobine shoulder morphology are seemingly intermediate between those of predominantly arboreal quadrupeds and well-known brachiators (Ashton and Oxnard 1964, Nakatsukasa 1994), and many colobine species are characterized by an absence or significant reduction of the pollex which some consider an adaptation for brachiation (Napier 1967, although see Morbeck 1979). Nevertheless, extensive field research has yielded virtually no instances of brachiation and only rare occurrences of bimanual suspension among both African (Mittermeier and Fleagle 1976, Morbeck 1977, 1979, McGraw 1996, Schubert 2011) and Asian (Ripley 1974, although see Workman and Covert 2005) colobines—underscoring the danger of interpreting primate positional behavior without field data.

Since the 1980s, the majority of positional behavior research has more explicitly addressed the influence of ecological variables—particularly forest architecture—on the expression of various positional behaviors. Fleagle and Mittermeier (1980) were among the first to directly consider ecological variables by predicting and testing relationships

among positional behavior, body size, substrate use, and forest strata. Others have expanded on this research (Fleagle 1980, Cant 1988, Gebo and Chapman 1995a, 1995b, McGraw 1998a, 1998b, 2000, Youlatos 1999) by reexamining these relationships and by considering additional positional behavior-environment interactions among numerous primate species. While universal claims concerning the relationship between positional behavior and forest architecture are not warranted, some general principles emerge: 1) larger supports are used more frequently for travel and smaller supports for foraging, 2) larger primates use larger supports more frequently than do smaller primates, 3) larger primates are predominantly constrained to forest strata with larger supports or to the ground, 4) smaller primates are not constrained as much by body size and thus exhibit more diverse positional behaviors and strata use compared to larger primates, and 5) leaping is more common during travel while climbing is more common during foraging (Fleagle and Mittermeier 1980, Gebo and Chapman 1995a, McGraw 1998a, Youlatos 1999).

Given the assumption that positional behavior is intricately linked to forest architecture, it is worth considering whether the positional behavior of a particular species differs between habitats characterized by markedly different forest compositions. Research examining this topic has yielded mixed results. In several taxa, positional behavior and support use were conserved across habitat types (Garber and Pruetz 1995, McGraw 1996, Manduell et al. 2012) while, other taxa appear to have exhibited significantly different positional behavior frequencies in distinct habitat types (Gebo and Chapman 1995b, Dagosto and Yamashita 1998, Schubert 2011).

Here I provide additional insight to this issue by examining the positional behavior of three troops of Angola black and white colobus monkeys (*Colobus angolensis palliatus*) inhabiting structurally distinct forest habitats of south coastal Kenya. While the majority of previous studies compared locomotor behaviors and support use across habitat types, I examined additional variables including postural behavior, activity budgets, and strata use in each forest habitat. Furthermore, this study addressed a criticism of comparative positional behavior studies: are the habitats structurally distinct enough to warrant valid comparisons (McGraw 1996)? In order to investigate this question, I quantified differences in forest structure and tree species composition among the three forest habitats.

First I tested the null hypothesis that *C. a. palliatus* troops from distinct forest habitats would exhibit no significant differences in activity budget. I predicted that given the dramatic differences in forest composition, activity budgets would likely differ between forest sites. Previous research has shown that *C. guereza* (Onderdonk and Chapman 2000, Chapman et al. 2007) and *C. vellerosus* (Wong and Sicotte 2007) exhibited different activity budgets in forests characterized by varying levels of degradation and fragmentation.

Next I tested the null hypothesis that the three troops would show no significant differences in overall strata use. I predicted that all troops would spend the majority of their time in the upper strata as seen in other species of black and white colobus monkeys (McGraw 1994, Gebo and Chapman 1995a, McGraw 1998a).

Third, I tested the null hypothesis that support use would remain relatively consistent across habitat types. I predicted that support use would remain largely consistent across habitats as was seen in *Colobus polykomos* troops from distinct forest areas in Ivory Coast (McGraw 1996).

Finally, I tested the null hypothesis that positional behavior profiles would not differ significantly between habitat types. I predicted that, in general, both locomotor and postural profiles would remain consistent across distinct forest types as was documented in *C. polykomos* from Ivory Coast (McGraw 1996).

Chapter 2: Methods

Study Site

Kenya's Diani Forest is part of the Zanzibar-Inhambane Floristic Region stretching from Mozambique to Somalia. It is also part of the Eastern Arc Mountains and Coastal Forests area which is considered one of Conservation International's 25 Hotspots for Biodiversity with numerous endemic flora and fauna (Metcalf et al. 2009). The Diani Forest (figure 1) is located in the Kwale District of south coastal Kenya ($4^{\circ}15'30''$, $4^{\circ}35'30''$ S and $39^{\circ}35'00''$, $39^{\circ}34'30''$ E). As a narrow strip measuring roughly 10 km long by 0.5 km wide (area= 455 ha), the Diani Forest is one of the few remaining patches of coral rag forest (Anderson et al. 2007c; Metcalfe et al. 2009).

South coastal Kenya is characterized by two rainy seasons with lighter, infrequent rains in October-December, and heavier, more frequent rains occurring March-June (Mwamachi et al. 1995). The remaining months (January-February and July-September) are markedly drier with occasional rain showers and storms. Annual rainfall is variable, but averages 744 millimeters (Mwamachi et al. 1995). Temperature is relatively constant year round, reaching 35°C in dry seasons and falling to 28°C in the rainy seasons (Okanga et al. 2006). This area is exceptionally humid (80-100%) year round (Okanga et al. 2006).

Diani is home to a diverse primate community containing seven species: black and white colobus monkeys (*Colobus angolensis palliatus*), Sykes monkeys

(*Cercopithecus mitis albogularis*), vervet monkeys (*Chlorocebus pygerythrus*), yellow baboons (*Papio cynocephalus*), Kenya coast galagos (*Galago cocos*), small-eared galagos (*Otolemur garnettii lasiotis*), and humans (*Homo sapiens*). Although there are few published studies on the Diani primates (Moreno-Black and Naples 1977, Eley and Kahumbu 1997; Okanga et al. 2006) a local organization, Colobus Conservation (formerly: Wakuluzu Friends of the Colobus Trust) has been monitoring Diani's primate populations since 1997. While Colobus Conservation invests considerable time and effort in wildlife conservation and forest management, research on the behavior and ecology of black and white colobus monkeys, Sykes monkeys, and vervet monkeys is also on-going.

The Diani area is a location of major infrastructural development with mining and tourist industries presenting major threats to forest and wildlife conservation. Despite its high biodiversity and conservation value, the Diani Forest is not gazetted as a reserve or national park, but divided into numerous private lots. This allows individual property owners to clear areas of forest at their discretion. Indigenous trees and shrubs are often replaced by expansive green lawns or exotic trees and flowering plants. After decades of anthropogenic disturbance, the Diani Forest now represents a continuum of degradation.

I examined troops inhabiting three areas of the Diani Forest. These areas are referred to as Baobab (figures 12-14), Colobus Trust (figures 15-16), and Kaskazi (figures 17-19) and have generally been described as a gradient from relatively pristine (Baobab), disturbed (Colobus Trust), to heavily degraded forest (Kaskazi) (Donaldson pers. comm.). A major roadway also bisects the forests that, in addition to dividing

previously contiguous canopy, result in dozens of animal-vehicle collisions annually. Furthermore, poorly insulated electrical lines often prove fatal for Diani's wildlife, with arboreal primates particularly vulnerable (figure 20).

Study Species

The Angola colobus (*Colobus angolensis*) is common throughout equatorial Africa and is typically divided into six subspecies: *C. a. angolensis*, *C. a. cordieri*, *C. a. cottoni*, *C. a. palliatus*, *C. a. prigoginei*, and *C. a. ruwenzorii*. Peters' Angola colobus (*C. a. palliatus*), the subject of this study, is found in a variety of forest habitats throughout much of Tanzania and the Kwale District of south coastal Kenya. The IUCN classifies *C. a. palliatus* under the category of least concern; however, in Kenya, the subspecies is recognized as endangered with likely fewer than 3,000 individuals remaining (Anderson et al. 2007c). Furthermore, recent mitochondrial DNA analyses suggest that *C. a. palliatus* from Kenya and northeastern Tanzania should be considered a distinct subspecies from the more numerous central Tanzanian forms. This highlights the need for immediate conservation initiatives (McDonald and Hamilton, 2010).

Angola colobus are medium sized, sexually dimorphic (females: 7.1 kg, males: 8.9 kg), long-tailed, and brilliantly colored monkeys (Bocian and Anderson in press). Although very few studies have been conducted on *C. a. palliatus* (figure 2), they show similarities with other colobines in terms of a predominantly (although not exclusively) folivorous diet and energy conservative lifestyle (Lowe and Sturrock 1998, Wijtten et al. 2012). Like other black and white colobus monkeys, the study species is highly arboreal

and is noted for its spectacular leaping ability (Rose 1973, 1979, Moreno-Black and Naples 1977, Gebo and Chapman 1995a). Group size at Diani averages 6 individuals with groups typically consisting of one adult male, and multiple adult females and their offspring (Donaldson pers. comm.). Larger groups of ten or more individuals, including two or more adult males are also present. Colobus density is extremely high at Diani leading to frequent intergroup encounters (Anderson et al. 2007c).

Habitat Description Methods

Differences in the forest structure of the three sites were assessed by surveying the forest areas used by each of the colobus troops during the study period. Because the Diani Forest is composed of numerous properties often divided by stone walls and bushes, it was easy to subdivide large blocks of forest into smaller discrete areas. For each area, all trees over 10 cm DBH (n= 3,051) were measured and plotted using a portable GPS device (Ganzhorn 2003). Variables recorded include: tree species name, classification as indigenous or exotic, DBH (measured with a tape measure), and tree height (estimated in 5 m increments).

Behavioral Sampling Methods

Positional behavior and support use of three troops of *C. a. palliatus* were recorded from June to August 2012. All three troops were habituated to human observers and were followed on a weekly (4-6 days per week) rotational basis. Data were collected from when the monkeys arose (typically 6:00) to when they settled into a sleeping tree

(roughly 18:00). Each group contained at least one adult male, at least two adult females, and a combination of sub-adults, juveniles, and infants. For each troop, members were individually identified and data were recorded for one adult male and two adult females. Data were recorded instantaneously at 3 minute time intervals, with at least 15 minutes between samples of the same individual to safeguard against potential auto-correlation of data points (C. Janson, personal communication in McGraw 1996). At each 3 minute interval the following were recorded: maintenance activity (i.e., feeding, foraging, resting, socializing, traveling), positional behavior (Tables 1 and 2), support type (Table 3), strata use (i.e., ground, sapling, lower canopy, upper canopy, emergent layer), and tree species utilized by focal animal. In total, the data set consists of 4,134 sample points spanning approximately 340 hours.

Statistical Methods

Botanical Analysis

First I described tree species composition for each habitat type noting the ten most frequent tree species. I then calculated species richness, Shannon-Weaver Index, and Evenness Index to describe tree species diversity for each of the sites. I compared mean DBH among habitats using the nonparametric Kruskal-Wallis and Mann-Whitney *U*-Tests because the data are not normally distributed. I also compared relative frequencies of DBH categories (small= 10-29 cm, medium= 30-49 cm, large \geq 50 cm) among habitat types using G-tests of interdependence (Sokal and Rohlf 1981). Similarly, I compared

tree height categories (small= 5 m, medium= 10 m, large \geq 15 m) using G-tests of interdependence.

Behavioral Analysis

I compared the positional behavior and support use of adult male and females from the same habitats using two-tailed ANOVAs. Alpha levels of 0.05 were used for all statistical tests. Because there were no significant differences between adult male and adult female positional behavior within any of three habitats, I pooled these behaviors for inter-habitat comparisons.

To test for differences in positional behavior among the three habitat types, I used G-tests of interdependence to compare overall locomotor and postural profiles (Sokal and Rohlf 1981). When significant differences were present, I used two-tailed ANOVAs to compare the frequencies of individual positional behavior categories. Overall support use, activity budgets, and strata use were compared using G-tests of interdependence. All statistical tests were performed using SAS 9.3 statistical software.

Chapter 3: Results

Habitat Results

Baobab

The Baobab study area was contained within one large plot measuring 10.5 ha in area. The western two-thirds of the plot was dominated by *Combretum schumannii* and *Fernandoa magnifica* trees and represented some of the tallest and most pristine canopy remaining in Diani (figure 12). Although not sampled quantitatively, the understory and edges of the more pristine forest contained dense patches of shrubs and climbers including *Premna hildebranti* and *Uvaria acuminata* (figure 13). The eastern one-third of the plot is immediately adjacent to the ocean and was characterized by several hotel buildings and a few in ground pools lined with the exotic *Cocoa nucifera*. A mix of indigenous and exotic tree species provided canopy connectivity to building rooftops (figure 14).

The ten most common tree species for the Baobab area are listed in Table 4. This area had the highest overall tree species richness (S=83), indigenous tree species richness (S=58), and exotic tree species richness (S=25) (figure 3). In terms of individual trees, the Baobab area also had the largest percentage of indigenous trees at nearly 71% (figure 4). Baobab was among the most diverse areas with the highest Shannon-Weaver Index and an intermediate Evenness Index (Table 8).

Baobab was the largest of the three areas and contains the highest number of trees (n= 1,412); however, tree density was intermediate (Table 7). In general, Baobab contained more large trees than the other two areas. Mean DBH (31 cm) was largest here, with significant differences between Baobab and Colobus Trust ($p < 0.0001$) but not between Baobab and Kaskazi (Table 9, figure 5). Overall comparisons of DBH categories and tree height categories revealed significant differences among all sites. Baobab contained higher frequencies of trees with DBH ≥ 50 cm (Table 10) and heights ≥ 15 m as seen in Table 11.

Colobus Trust

The Colobus Trust area was composed of several smaller properties totaling 7.37 ha in area. Properties were variable in terms of tree species composition, nature of understory, and height of main canopy. All of the properties contained one or more private houses—many of which are empty for several months out of the year (figure 16).

Overall, this forest area was dominated by exotic tree species, with the exotic *Azadirachta indica* and *Delonix regia* comprising more than half of all trees sampled (n=1,045) (figure 4). Of all the trees sampled at Colobus Trust, fewer than 32% of them were indigenous. The top ten most common tree species are reported in Table 5. Although this forest area contained at least 69 species of trees (45 indigenous and 24 exotic), the ten most common constituted more than 80% of all trees sampled. Colobus Trust exhibited the lowest diversity scores for Shannon-Weaver Index and Evenness Index (Table 8).

Colobus Trust was the second largest area and contained the second greatest number of trees, but the greatest density of trees (141.84 trees/ ha) (Table 7). Mean DBH (25 cm) was significantly lower than mean DBH at the other two sites as seen in Table 9 and figure 5. Overall comparisons of DBH categories revealed that Colobus Trust contained a higher frequency (74.5%) of small (10-29 cm DBH) trees (Table 10). Overall comparisons of tree height profiles revealed the majority of tree species were in the medium height range of 10 m (Table 11, figure 6).

Kaskazi

Roughly 90% of the Kaskazi troop's time was spent in one relatively large plot (figure 18) characterized by a mix of indigenous and exotic trees, grass, exotic flowers, and the maintenance area and junkyard of the Kaskazi Hotel (figure 19). The property adjacent to the south was largely made up of thick secondary growth with a few large trees emerging from the understory. This was without a doubt among the most degraded portions of the Diani Forest. In total, this area covered just over 5 ha and contained the fewest number of trees (n= 597) and smallest tree density (119.1 trees/ha) of any area sampled (Table 7).

The three most common tree species at Kaskazi were all exotic species, but these three combined only account for 31.8% of all trees sampled here. Table 6 reports the ten most frequent tree species. Roughly half of all trees sampled were indigenous and half were exotic (53.8% and 46.2% respectively) (figure 4). While Kaskazi had the lowest overall tree species richness (S=61), indigenous richness (S=40), and exotic richness

(S=21), it had the highest Evenness Index due to the fact that no single or handful of species dominated the area (Table 8). The Shannon-Weaver Index of diversity was intermediate to Baobab and Colobus Trust.

Mean DBH (28 cm) was significantly larger than at Colobus Trust ($p < 0.0001$) and smaller than at Baobab although this difference was not significant (Table 9, figure 5). Overall comparisons of DBH categories demonstrated that 94.9% of Kaskazi's trees ranged between 10 and 49 cm. Kaskazi was intermediate to Baobab and Colobus Trust for every DBH category (Table 10). Overall height comparisons revealed that Kaskazi was significantly different from the other two habitats with only 10.4% of trees ≥ 15 m in height compared to 17.2% for Colobus Trust and 26.7% for Baobab (Table 11, figure 6).

Behavioral Results

Activity Budgets

Table 12 and figure 7 show comparisons of maintenance activities among the three troops. Activity budgets followed the same general trend for all groups with resting (58.9-66.0%) followed by feeding (21.8-28.0%) as the most common behaviors. Traveling (3.6-7.6%) and socializing (2.4-5.0%) were less common while foraging was especially rare (1.0-2.3%) in all troops. For statistical tests, foraging was merged with feeding due to very small sample size.

Comparisons of overall activity budgets revealed significant differences between all groups ($p < 0.0001$ for all comparisons). Most notably, the Baobab troops spent more time feeding and moving, and less time resting compared to the other troops. The

Kaskazi troop spent the most time resting and socializing with the lowest percentages of time spent traveling and feeding. The Colobus Trust troop was intermediate in virtually every behavioral category.

Strata Use

Overall strata use for each troop is shown in Table 13 and figure 8. Significant differences were present for every comparison of overall strata use ($p < 0.0001$ for all comparisons). Time spent on the ground was less than 1% for all troops. Similarly, use of emergent stratum constituted a small percentage (0.28-2.1%) for all troops. The troops were considerably more variable in terms of time spent at the sapling level (15.8-30.2%), lower canopy (30.5-48.0%), and upper canopy (31.5-45.0%). In general, the Colobus Trust troop spent more time in the upper canopy (45.0%), the Kaskazi troop in the lower canopy (48.0%), and the Baobab troop was relatively even across sapling (30.2%), lower canopy (30.5%), and upper canopy (38.2%) strata.

Table 14 shows percent of maintenance activities at different strata for each troop, however, no statistical tests were run on these relationships. In general, traveling was variable and occurred in the sapling layer (15.3-35.7%), lower canopy (27.8-45.8%), and upper canopy (12.5-35.2%). Foraging occurred primarily in the sapling layer (46.9-56.23%) with lower frequencies reported in the lower (9.4-37.5%) and upper canopy (6.25-37.5%). In Kaskazi and Colobus Trust troops, feeding occurred relatively equally between sapling layer (31.8-33.8%), lower canopy (30.3-37.4%), and upper canopy (30.0-35.1%); however, feeding occurred most frequently in the sapling layer (51.0%)

with lesser instances in lower (25.3%) and upper canopy (21.5%) for the Baobab troop. Resting occurred primarily in the main canopy (i.e., lower and upper canopy) for all troops (79.3-90.2%). Lastly, social activity took place primarily in the lower (26.3-57.1%) and upper canopy (35.1-65.8%) for all troops.

Support Use

Frequencies of support use for each troop are reported in Table 15 and figure 9. Comparisons of overall support use revealed no differences for Colobus Trust vs. Kaskazi troops, however, significant differences are reported for Colobus Trust vs. Baobab ($G=47.573$, $p<0.0001$.) and for Kaskazi vs. Baobab ($G=39.638$, $p<0.0001$). The Baobab troop utilized fewer boughs (32.9%), compared to Colobus Trust (42.6%) and Kaskazi (42.0%) and more branches (57.1%) and twigs (6.2%) than Colobus Trust (48.7%, 3.1%) and Kaskazi (49.5%, 3.4%). All troops used manmade supports relatively equally (3.8-5.6%).

Support use during maintenance activities is shown in Table 16. Statistical tests were not run on these relationships because it is not central to the argument of this paper. In general, ground, vertical trunks, and manmade supports were used infrequently during all maintenance activities. Travel occurred most frequently on boughs (28.7-40.3%) and branches (43.1-51.9%) for all groups. The majority of foraging was done on branches (55.0-81.3%), although foraging also occurred at varying frequencies on boughs (9.5-30.0%) and twigs (6.3-18.8%). Feeding took place primarily on branches (67.4-76.4%) with smaller frequencies on boughs (6.3-14.2%) and twigs (10.4-13.9%). Resting

occurred primarily on boughs (42.7-53.4%) and branches (40.4-51.4%). Finally, social activity occurred largely on boughs (48.6-68.4%) and branches (26.3-42.8%).

Locomotor Behavior

Table 17 and figure 10 show inter-habitat comparisons of locomotor behaviors. For statistical tests, locomotor categories were pooled into three categories: climbing, leaping, and quadrupedal locomotion (includes: bounding, quadrupedal running, and quadrupedal walking). Comparisons of overall locomotor profiles revealed non-significant differences for Colobus Trust vs. Kaskazi and Kaskazi vs. Baobab, but significant difference for Colobus Trust vs. Baobab ($G=7.19$, $p=0.027$). Comparisons of individual locomotor behaviors, however, showed no significant differences between climbing, leaping, or quadrupedalism for Colobus Trust vs. Baobab, but showed a significant difference in the time spent climbing for Colobus Trust vs. Kaskazi ($p=0.0088$). Across all habitats, quadrupedal walking was the predominant locomotor mode (44.4-45.7%), percentages of leaping were nearly identical (16.3-16.7%), but percentages of bounding (18.7-30.4%) and climbing (6.5-18.0%) were more variable.

Locomotor behaviors in relation to maintenance activities are shown in Table 18. No statistical tests were run on these comparisons, but general results are described. Quadrupedal walking was the most common locomotor behavior for all troops during foraging (55.0-71.9%). Climbing (15.0-18.8%) and leaping (6.3-20.0%) occurred to lesser extents. For travel, quadrupedal walking was the most frequent locomotor behavior (37.0-43.1%) followed by bounding (23.2-36.1%). Leaping occurred

consistently (15.3-19.6%) while climbing was more variable (4.2-18.5%) among the three troops during travel.

Postural Behavior

Table 19 and figure 11 display postural behavior for each troop. For statistical tests, recognized categories were sit, stand (pooled quadrupedal stand and supported stand), and lie (pooled prone lie and recline) behaviors. Overall postural comparisons yielded non-significant results for Colobus Trust vs. Baobab but significant differences for Colobus Trust vs. Kaskazi ($G=24.351$, $p<0.0001$) and for Kaskazi vs. Baobab ($G=17.455$, $p=0.0002$). Comparisons of individual postural behaviors indicated that time spent standing was significantly greater at Baobab (1.1%) vs. Colobus Trust (0.57%) ($p=0.0371$). The Kaskazi troop sat less frequently (85.3%) than the Baobab troop (90.7%) ($p=0.0040$) and also spent more time lying (13.1%) than the Baobab troop (8.3%) ($p=0.0022$). In general, sitting was by far the most frequent (85.2-91.2%) positional behavior used by all three troops. Prone lying (5.1-6.7%) and reclining (2.7-6.5%) constituted lesser percentages while quadrupedal standing (0.43-1.2%) and supported standing (0.14-0.24%) were especially rare in all troops.

Postural behaviors in relation to maintenance activities are reported in Table 19. No statistical tests were performed on these relationships; however, general results are reported. Sitting was the primary feeding posture (97.6-98.5%) for all groups. Sitting was also the most common posture during resting (85.1-88.8%), followed by prone lying (7.1-8.7%) and reclining (3.3-5.8%). Postures used during social activity were more

variable, but sitting (46.8-85.71%), reclining (11.43-41.6%), and prone lying (7.8-10.5%) represented the most common postures.

Chapter 4: Discussion

Activity Budgets

As predicted, overall activity budgets differed significantly among all troops (Table 12). Of course, this does not imply that all pairwise comparisons of individual maintenance activities differed significantly. The largest discrepancy between any two behaviors was an 8.3% increase in time spent resting at Kaskazi compared to Baobab. The higher frequency of resting and lower frequencies of feeding and moving at Kaskazi likely relate to living in one of the most degraded areas of the Diani Forest. Similar instances of elevated inactivity and movement were reported in other black and white colobus monkey species inhabiting fragmented and degraded forests (Onderdonk and Chapman 2000, Chapman et al. 2007, Wong and Sicotte 2007).

Numerous studies have shown that black and white colobus monkey activity budgets vary greatly across species and forest types (see Fashing 2007). Resting is generally the most frequent activity for most black and white colobus monkey groups but ranges from 71% of daily activity in *Colobus vellerosus* (Wong and Sicotte 2007) to 32% in *C. angolensis* (Fashing et al. 2007). Other behavioral categories are also highly variable: traveling (2% in *Colobus guereza* to 24% in *Colobus angolensis*), feeding (17-42% in different groups of *C. guereza*), and socializing (1% in *C. polykomos* to 14% in *C. satanas*) (McKey and Waternab 1982, Dasilva 1989, 1992, Bocian 1997, Onderdonk and Chapman 2000, Fashing 2001, Chapman et al. 2007). The Diani troops fell within these

ranges for all maintenance activities, but significantly differed from each other in overall activity budgets. Undoubtedly there are a multitude of reasons as to why these activity budgets differed between groups, but differences in food availability (due to significant differences in forest composition and structure) and pressures from neighboring colobus groups (as a result of unusually high colobus population density) are likely major factors constraining activity budgets at Diani (Anderson et al. 2007a).

Strata Use

I predicted that strata use would not differ between colobus troops; however comparisons of overall strata use yielded significant differences between all groups. In general, all groups spent the majority of their time (60.7-82.7%) in the main canopy (i.e., lower and upper canopy), however, the Baobab troops spent nearly twice as much time in the sapling layer (30.2%) compared to the other two groups (15.8-17.8%). This is likely because much of the understory and sapling layer have been cleared in portions of the Colobus Trust (figure 16) and Kaskazi areas (figure 18). At the same time, the Baobab study area contained the largest and most intact canopy (figure 12). Thus, these results suggest that the Baobab troop actively chose the sapling layer more frequently.

When examining maintenance activities at different strata some general trends emerged: 1) foraging was most common in the sapling layer for all troops 2) feeding was common in the sapling layer, lower canopy, and upper canopy 3) resting and socializing occurred more frequently in the main canopy. I did not collect data on food availability at different strata, but these results suggest preferred food items were more abundant in

lower strata at Baobab and relatively equally dispersed through the main canopy and sapling layers at the other two sites. It is possible that the monkeys spent more time resting and grooming at higher canopy levels as a means of reducing predation risk associated with lower strata (Youlatos 1999). Although there are few natural predators in modern day Diani (leopards are locally extinct and large birds of prey are rare), dogs, baboons, and automobiles pose the greatest threats to black and white colobus monkeys and likely deterred them from spending more time on the ground and in lower strata.

Support Use

I predicted that support use would be consistent among all troops. While overall support use was virtually identical for the Colobus Trust and Kaskazi troops, both differed significantly from the Baobab troop with the latter utilizing fewer boughs and more branches and twigs. McGraw (1996) found that *Colobus polykomos* from the Tai Forest preferred large supports (i.e., use more frequently than predicted based solely on abundance) for most behaviors. Because the Baobab habitat is characterized by the largest concentration of large trees in terms of mean DBH, frequency of trees with DBH ≥ 50 cm, and trees with height ≥ 15 m, it is reasonable to assume this habitat would also have the highest abundance of large supports. Thus, one would predict that the Baobab troop would utilize boughs more than or as frequently as the other troops from forest areas characterized by smaller trees; I found just the opposite. This phenomenon is almost certainly related to the Baobab troop's affinity for feeding on *Premna hildebrandtii*—an indigenous plant that grows in thick, tangled clusters of thin supports

(figure 30). This plant was common in the understory but also climbed into the canopy of larger trees. On several occasions, the Baobab troop fed on the leaves, flowers, and fruits of this plant for nearly an hour and then rested among the tangled supports often for hours thereafter. This plant, virtually absent from the Colobus Trust and Kaskazi sites, constituted the largest portion of the Baobab troop's diet (28.9%) compared to less than 1% of the diets at the other locations (Dunham unpublished data). It is likely that the high density of these small supports actually provided a solid and stable platform on which to feed and rest. For future studies it would be useful to differentiate individual/small groupings of thin supports that deform under an animal's body weight from those that are clustered tightly together and do not deform.

When looking at support type in relation to maintenance activities some general trends emerged. 1) Moving, resting, and socializing usually occurred on large supports (i.e., boughs and branches) most likely because these behaviors require enhanced stability. 2) Feeding and foraging took place most often on branches rather than boughs. This was likely the case because branches allow access to food items located on the terminal ends of supports (Cant 1992, McGraw 1998a; 1998b). It is likely that branches were preferred over twigs because they provided greater stability when feeding. 3) Non-natural supports (especially rooftops) were used by all troops for traveling and to a lesser extent for all maintenance activities.

Locomotor Behavior

I predicted that locomotor behavior would be consistent across habitat types. Although between site comparisons yielded statistically significant differences in the overall locomotor profiles of Baobab and Colobus Trust troops and frequencies of climbing between Colobus Trust and Baobab, locomotor behaviors were for the most part consistent across habitats. For instance, all troops demonstrated a propensity for the same locomotor behaviors: bound, climb, leap, quadrupedal walk, and quadrupedal run. Furthermore, this study corroborates results from previous studies on other black and white colobus species in which no instances of arm swinging were observed (Mittermeier and Fleagle 1976, Morbeck 1977, 1979, McGraw 1996, Schubert 2011). Instead, pronograde locomotor modes (quadrupedal walking and bounding) constituted 64-76% of locomotor behaviors with lesser and relatively equal frequencies of climbing and leaping. The slight differences in locomotor behaviors between troops are likely related to overall support use (Prost 1965, McGraw 1998a). At Colobus Trust, a greater frequency of main canopy bough use provided stable supports for bounding. In contrast, the Baobab troops spent more time moving and foraging on small, densely packed clusters of supports in the sapling layer that do not facilitate bounding but require climbing to navigate.

Examining locomotion by maintenance activity revealed some general trends across habitat types. In general: 1) bounding and leaping occurred more frequently during travel and 2) quadrupedal walking and climbing were more frequent during foraging. These results are consistent with those reported by other researchers (Fleagle and Mittermeier 1980 Gebo and Chapman 1995a, McGraw 1998a) and are intuitive since foraging monkeys are more likely to adopt slower, more deliberate locomotor modes

(e.g., climbing and quadrupedal walking) when searching for and processing food (Cant 1992). In contrast, monkeys traveling from one food patch to another are more likely to seek relatively direct paths, utilize quicker locomotor modes (e.g., bounding), and should encounter more canopy discontinuities that require gap-crossing behaviors (e.g., leaping) (Cant 1992).

Postural Behavior

As predicted, postural behaviors were generally consistent across different habitats, despite a few statistically significant differences between troops. As demonstrated in previous studies (Mittermeier and Fleagle 1976, Morbeck 1977, 1979, Rose 1979, Gebo and Chapman 1995a, McGraw 1998b), sitting constituted the overwhelming majority of black and white colobus monkey postural behavior with 85-91% of all postural behaviors reported for the Diani troops. After sitting, the three troops followed the same trend in which time spent prone lying > reclining > quadrupedal standing > supported standing.

When considering postural behavior used during different maintenance activities, several trends emerged across habitat types: 1) sitting was the most common postural behavior used during feeding, resting, and socializing 2) sitting was almost the only posture used during feeding (97-98% for all troops) 3) prone lying, and to a lesser extent, reclining were frequent resting postures 4) reclining, and to a lesser degree prone lying, were common postures adopted during social activity (e.g., grooming). The Kaskazi troop exhibited significantly higher percentages of time spent prone lying and reclining,

especially during rest and social behaviors. It is possible that this was an energy conservation strategy suited to this highly degraded portion of the Diani Forest. Dietary and daily path length information on this troop has shown they are traveling shorter distances per day while eating less high-quality food items (i.e., fruits, seeds, and flowers) compared to the Baobab and Colobus Trust troops (Dunham, unpublished data).

Behavioral Flexibility and the Conservative Nature of Positional Behavior

In contrast to many other primate taxa including closely related red colobus (*Procolobus*), black and white colobus monkeys readily adapt to altered forest environments. In addition to inhabiting primary forest throughout Africa, black and white colobus monkeys inhabit secondary forest and degraded forest fragments, often at higher densities than in primary forests (Onderdonk and Chapman 2000, Anderson et al. 2007a, 2007b, Chapman et al. 2007, Wong and Sicotte 2006, Mammides et al. 2008). Their success in disturbed environments relates to their behavioral and dietary flexibility (Marsh 2003). Black and white colobus monkeys are able to utilize very small home ranges (Fashing et al. 2007) and adapt to food scarcity by resting more and traveling less per day (Onderdonk and Chapman 2000, Harris and Chapman 2007). Behavioral flexibility with regards to activity budgets was already described above.

Although the traditional view of black and white colobus monkeys comes from studies on *C. guereza* in which diet is dominated by leaves (up to 94%) (Harris and Chapman 2007) with as much as 88% of feeding observation coming from a single tree species (Clutton-Brock 1975), this generalization fails to characterize the broad dietary

variation among this taxon. While once viewed as obligate folivores, subsequent studies reveal that black and white colobus monkeys rely heavily on fruits and seeds (Dasilva 1994, Korstjens et al. 2006) lichens, (Fashing et al. 2007), and other food items (Fashing 2007) throughout their ranges.

This study demonstrated that overall activity budgets, strata use, and to a lesser extent support use of *C. a. palliatus* vary across structurally distinct forest habitats. More importantly, although these behaviors differed significantly between troops, both locomotor and postural behaviors were generally consistent. McGraw (1996) argued that one way locomotor modes are conserved across structurally different habitats is by primates consistently choosing the same support types despite differences in their availability. Support types, in turn, limited the kinds of locomotor behaviors that can be performed. More recent research (Bitty and McGraw 2007) suggested that sympatric and closely related guenons exhibit consistent positional behavior profiles despite significant differences in support use, however. Similarly, Garber and Pruetz (1995) have shown that positional behavior is largely conserved despite discrepancies in support use. While positional behaviors are intricately linked to the kinds of supports utilized, I argue that morphology, in a more general sense, is likely the key variable constraining positional behavior.

The conservation of positional behaviors across forest types has been documented in several species both in the New World and the Old World (Garber and Pruetz 1995, McGraw 1996, Manduell et al. 2012). At the same time, a handful of taxa exhibit significantly different positional behavior frequencies in distinct forest types (Gebo and

Chapman 1995b, Dagosto and Yamashita 1998, Schubert 2011). There are a number of potential explanations for these discrepancies.

First, some argue that studies (including this one) that find no differences in locomotor or postural behavior between forest types simply compare habitats that are not structurally dissimilar enough to warrant positional behavior differences (McGraw 1996). Although I did not quantify availability of different sized supports as others have done (McGraw 1996, Dagosto and Yamashita 1998, Manduelli et al. 2012), the dramatic differences in tree species composition, DBH and height categories, and tree density coupled with significant differences in activity budgets and strata use between the three forest patches strongly suggest that these three forest habitats are indeed structurally distinct.

Differences in behavioral data collection methods may also play a role in why some studies find significant positional behavior differences between environments. For instance, it is well documented that the two primary positional behavior data collection methods (i.e., instantaneous sampling and continuous bout sampling) produce different positional behavior profiles (Dagosto and Gebo 1998). Even if a study employs the same general behavior collection method across study sites, however, differences in how positional behavior categories are defined (e.g., climbing: see Hunt et al. 1996; Dagosto and Gebo 1998) and other inter-observer errors (Gebo and Chapman 1995a) may lead to statistically different results.

Another potential discrepancy raised by Dagosto and Yamashita (1998) concerns statistical methods and interpretation. Garber and Pruetz (1995) and McGraw (1996)

compared overall positional behavior profiles via non parametric rank order statistics and G-tests of interdependence respectively and found no significant differences between habitat type. Gebo and Chapman (1995a) and Dagosto and Yamashita (1998), on the other hand, found significant differences when comparing the frequency of individual positional behavior categories using ANOVAs. In this study I showed that statistical tests of overall positional behavior profiles (i.e., G-tests) do not necessarily corroborate tests on the frequency of individual behaviors (i.e., ANOVA). The issue of differentiating statistical significance from biological significance, therefore, remains a fairly subjective endeavor. For instance, although the time spent standing between the Colobus Trust troop (0.57%) and the Baobab troop (1.1%) was statistically different, I do not consider this difference biologically meaningful. I use similar lines of reasoning to conclude that the other few statistically significant differences in locomotor and postural behaviors were not distinct enough to question the general assertions of the form-function complex (Bock and von Wahlert 1965).

Finally, it is likely that species respond differently to changes in habitat structures; some may be more behaviorally flexible, not only with regard to diet, activity budget, strata use, and support use, but also in their positional behavior. More intraspecific studies, particularly those examining structurally distinct habitats are required to discern whether some species are more flexible in their positional behavior repertoires than others, and if this is the case, what factors (e.g., morphology, social structure, diet, predation avoidance, etc.) lead to this phenomenon.

Directions for Future Study

Future studies could examine a large variety of positional behavior related issues. First, additional data on *C. a. palliatus* positional behavior and habitat use over different seasons and in relation to food availability would provide stronger evidence concerning to what extent positional behavior is conserved across habitat types. Likewise, assessing the positional behavior of sympatric *Cercopithecus mitis albogularis*, *Chlorocebus pygerythrus*, and *Papio cynocephalus* in distinct forest areas would also enhance our understanding of this issue while simultaneously providing a more holistic view of the positional behavior and habitat use for the Diani primate community.

Future studies should also combine behavioral data with morphological and histological analyses of post cranial material from Diani's primates. It is likely that examining multiple avenues will provide a more intimate understanding of ecological and morphological constraints on positional behavior.

Chapter 5: Conclusion

This study suggests that differences in forest structure and ecological variables between three areas of the Diani Forest facilitate significant differences in overall activity budgets, strata use, and support use to a lesser extent. At the same time, both locomotor and postural behaviors are largely consistent across habitat types. Although environment surely influences positional behavior to some extent, these results suggest that morphology likely plays a greater role in constraining positional behavior of *C. angolensis palliatus*.

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Appendix A: Tables

Table 1. Description of locomotor behaviors

Quadrupedal Walk	relatively slow, pronograde quadrupedal locomotion
Quadrupedal Run	faster version of quadrupedal walk, includes diagonal sequence gaits and galloping
Bound	quadrupedal pronograde locomotion in which the both hindlimbs contact simultaneously followed by both forelimbs contacting simultaneously (usually rapid movement but not always)
Leap	locomotion between discontinuous supports characterized primarily by hindlimb extension with landing including hindlimbs and/or forelimbs
Climb	vertical or near vertical (support angle greater than 45°) ascent in which forelimbs reach above head and hind limbs push the animal up
Arm Swing	locomotion involving forelimb suspension (e.g., brachiation, bimanualism)

Table 2. Description of postural behaviors

Sit	Posture in which ischia bear a majority of body weight with torso relatively orthograde
Stand	All four limbs extended on a relatively horizontal support with torso pronograde
Supported Stand	Standing posture in which at least two limbs are extended on a relatively horizontal support with one or more limbs flexed or reaching out; torso may be orthograde or pronograde
Prone Lie	Lying posture with majority of body weight on the ventral surface; limbs may be dangling below support or tucked under body
Recline	Lying posture with majority of body weight on dorsum or lateral aspect of torso
Forelimb Suspension	Below-support arm hanging posture using one or more appendages
Cling	Flexed limb posture on relatively vertical supports

Table 3. Description of support types

Bough	Large supports, greater than 10 cm in diameter and large enough that adult monkeys cannot fully grasp with hands or feet
Branch	Medium-size supports, between 2 and 10 cm in diameter and small enough for adult monkeys to grasp with hand and feet
Twig	Small supports, less than 2 cm in diameter and usually found on the terminal end of branches
Vertical Trunk	Vertical support of any diameter in which the monkey must cling
Manmade	Manmade supports of any size (e.g., rooftop, power line, wall)

Table 4. Top ten most abundant tree species in the Baobab area

Species	Indigenous or Exotic	n	% of forest
<i>Combretum schumani</i>	I	263	18.63%
<i>Cocoa nucifera</i>	E	125	8.85%
<i>Fernandoa magnifica</i>	I	93	6.59%
<i>Hunteria zeylanica</i>	I	75	5.53%
<i>Caryota urens</i>	E	68	4.82%
<i>Lecaniodiscus franxinifolius</i>	I	68	4.82%
<i>Lansea welwischii</i>	I	54	3.82%
<i>Pycnocomia littoralis</i>	I	48	3.40%
<i>Borrassus sp.</i>	E	44	3.12%
<i>Adasonia digitata</i>	I	38	2.69%
73 other species	x	536	37.96%

Table 5. Top ten most abundant tree species in the Colobus Trust area

Species	Indigenous or Exotic	n	% of forest
<i>Azadirachta indica</i>	E	405	38.76%
<i>Delonix regia</i>	E	133	12.72%
<i>Fernandoa magnifica</i>	I	88	8.42%
<i>Lannea welwischii</i>	I	61	5.84%
<i>Cocoa nucifera</i>	E	48	4.59%
<i>Dictyospermu album</i>	E	32	3.06%
<i>Plumaria rubra</i>	E	28	2.70%
<i>Adasonia digitata</i>	I	16	1.53%
<i>Zanthoxylum chelybeum</i>	I	14	1.34%
<i>Pandanus kirkii</i>	E	13	1.24%
59 other species	x	207	19.81%

Table 6. Top ten most abundant trees in the Kaskazi area

Species	Indigenous or Exotic	n	% of forest
<i>Cocoa nucifera</i>	E	100	16.84%
<i>Delonix regia</i>	E	46	7.74%
<i>Azadirachta indica</i>	E	43	7.24%
<i>Grewia plagiophylla</i>	I	39	6.57%
<i>Euphobia nyika</i>	I	33	5.56%
<i>Zanthoxylum chelybeum</i>	I	32	5.39%
<i>Lecaniodiscus franxinifolius</i>	I	29	4.88%
<i>Plumaria rubra</i>	E	18	3.03%
<i>Diospyros consolate</i>	I	17	2.86%
<i>Borrassus sp.</i>	E	14	2.36%
51 other species	x	223	37.54%

Table 7. General characteristics for each forest area

Location	Area	Trees Sampled	Trees/ ha	DBH/ ha
CT	7.3673	1045	141.84	3550.96
KK	5.0147	597	119.05	3325.62
BH	10.4884	1412	134.62	4167.84

Table 8. Diversity measures for each forest area

Forest Type	[S]	[H]	[E]
CT	69	2.586	0.611
KK	61	3.336	0.811
BH	83	3.411	0.772

[S]: richness

[H]: Shannon-Weaver Index of Diversity

[E]: Evenness Index

Table 9. Comparisons of mean DBH

CT	<u>Mean</u>		<u>Kruskal-Wallis</u>	<u>Mann-Whitney U-Test</u>		
	KK	BH	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
25	28	31	73.697***	***	***	ns

Kruskal-Wallis test (df=2) post hoc Mann-Whitney U-test (df=1)

ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 10. Comparisons of DBH categories

Forest Type	DBH Categories			
	10-29 cm	30-49 cm	50-69 cm	70+ cm
CT	74.45	21.44	2.97	1.15
KK	65.32	28.79	4.71	1.18
BH	60.62	26.98	8.36	4.04

Values are percentages of trees by DBH category for each forest area

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	84.45	15.23	75.62	20.82
Critical X ² value	7.815 (.05)	5.991 (.05)	5.991 (.05)	5.991 (.05)
Significance	***	***	***	***

DBH categories pooled into three categories; see text for details
 ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 11. Comparisons of tree height categories

Forest Type	Tree Height Categories			
	5m	10m	15m	20m+
CT	31.39	51.39	16.17	1.05
KK	37.19	52.43	10.05	0.34
BH	35.84	37.46	24.08	2.62

Values are percentages of trees by height category for each forest area

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	106.151	16.563	54.526	80.544
Critical X ² value	7.815 (.05)	5.991 (.05)	5.991 (.05)	5.991 (.05)
Significance	***	***	***	***

Tree height categories pooled into three categories; see text for details
 ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 12. Comparisons of activity budget

Troop	Feed	Forage	Move	Rest	Social	Other	n
CT	25.41	1.35	4.86	66.01	2.36	0	1480
KK	21.83	1.04	3.63	67.16	4.99	1.36	1544
BH	28.03	2.34	7.64	58.88	2.69	0.42	1413

Values are percentages of time spent in various maintenance activities for each troop
 Feed and forage were combined into single category for statistical tests; other category omitted

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	64.845	11.097	18.481	55.603
Critical X ² value	12.592	7.815	7.815	7.815
Significance	***	***	***	***

ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 13. Comparisons of strata use

Troop	Ground	Sapling	Lower	Upper	Emergent	n
CT	0.61	15.81	37.7	45	0.88	1480
KK	0.71	17.75	47.99	31.48	2.07	1544
BH	0.92	30.15	30.5	38.15	0.28	1413

Values are percentages of time spent at various heights for each troop
 Feed and forage were combined into single category for statistical tests; other category omitted

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	173.449	56.635	85.087	115.186
Critical X ² value	9.488	5.991	5.991	5.991
Significance	***	***	***	***

Ground variable omitted for statistical tests

ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 14. Percent of time in maintenance activities at different strata

BH						
	Ground	Sapling	Lower	Upper	Emergent	n
Travel	3.7	33.33	27.78	35.19	0	108
Forage	6.25	46.88	9.38	37.5	0	32
Feed	1.77	51.01	25.25	21.46	0.51	396
Rest	0	21.41	34.21	45.14	0.24	833
Social	0	7.89	26.32	65.79	0	38
KK						
	Ground	Sapling	Lower	Upper	Emergent	n
Travel	7.14	35.71	44.64	12.5	0	56
Forage	0	56.25	37.5	6.25	0	16
Feed	0.59	31.75	37.39	29.97	0.3	337
Rest	0.39	12.83	50.72	33.27	2.8	1037
Social	1.3	5.19	57.14	35.06	1.3	77
CT						
	Ground	Sapling	Lower	Upper	Emergent	n
Travel	4.17	15.28	45.83	33.33	1.39	72
Forage	0	55	20	25	0	20
Feed	0.53	33.78	30.32	35.11	0.27	376
Rest	0.41	8.39	40.33	49.85	1.02	977
Social	0	8.57	34.29	54.29	2.86	35

Table 15. Comparisons of support use

Troop	Bough	Branch	Twigs	Manmade	n
CT	42.6	48.67	3.14	5.59	1467
KK	41.96	49.48	3.4	5.15	1530
BH	32.86	57.1	6.24	3.8	1394

Values are percentages of time spent on various support types for each troop

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	58.157	0.584	47.573	39.638
Critical X ² value	12.592 (.05)	7.815 (.05)	7.815 (.05)	7.815 (.05)
Significance	***	ns	***	***

Postural behaviors pooled into three categories; see text for details

ns: not significant * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 16. Percent of time in maintenance activities on different supports

	Ground	Trunk	Bough	Branch	Twig	Manmade	n
<u>Baobab</u>							
Travel	2.78	2.78	28.7	51.85	4.63	9.26	108
Forage	6.25	3.13	9.38	62.5	18.75	0	32
Feed	1.41	0.4	6.25	76.41	13.91	1.61	496
Rest	0	0.12	42.74	51.38	1.68	4.08	833
Social	0	0	68.42	26.32	2.63	2.63	38
<u>Kaskazi</u>							
Travel	7.14	8.93	26.79	48.21	1.79	7.14	56
Forage	0	0	12.5	81.25	6.25	0	16
Feed	0.59	0	14.24	67.36	11.87	5.93	337
Rest	0.19	0	50.14	43.88	0.96	4.82	1037
Social	1.3	0	58.44	40.26	0	0	77
<u>Colobus Trust</u>							
Travel	4.17	1.39	40.28	43.06	1.39	9.72	72
Forage	0	0	30	55	10	5	20
Feed	0.53	0.53	13.56	69.68	10.37	5.32	376
Rest	0.31	0	53.43	40.43	0.61	5.22	977
Social	0	0	48.57	42.86	0	8.57	35

Table 17. Comparisons of locomotor behavior

Troop	AS	B	CL	L	QR	QW	Other
CT	0	30.43	6.52	16.3	1.09	45.65	0
KK	0	23.61	15.28	16.67	0	44.44	0
BH	0	18.71	17.99	16.55	1.44	44.6	0.72

Values are percentages of time spent in various locomotor behaviors for each troop

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	7.35	3.438	7.19	0.284
Critical X ² value	7.815 (.05)	5.991 (.05)	5.991 (.05)	5.991 (.05)
Significance	ns	ns	*	ns

Locomotor behaviors pooled into three categories; see text for details

ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

	CT vs. KK	CT vs. BH	KK vs. BH
Quad	ns	ns	ns
Climb	**	ns	ns
Leap	ns	ns	ns

ANOVAs for different locomotor behaviors

Locomotor behaviors pooled into three categories: quadrupedalism, leaping, and climbing

ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 18. Percent of time in locomotor behavior by maintenance activity

	AS	B	CL	L	QR	QW	Other	n
<u>Baobab</u>								
Forage	0	3.13	15.63	9.38	0	71.88	0	32
Travel	0	23.15	18.52	18.52	1.85	37.04	0.93	108
<u>Kaskazi</u>								
Forage	0	0	18.75	6.25	0	75	0	16
Travel	0	30.36	12.5	19.64	0	37.5	0	56
<u>Colobus Trust</u>								
Forage	0	10	15	20	0	55	0	20
Travel	0	36.11	4.17	15.28	1.39	43.06	0	72

Table 19. Comparison of postural behavior

Forest Type	PL	R	S	SS	ST	Other
CT	5.48	2.74	91.21	0.14	0.43	0
KK	6.66	6.45	85.26	0.2	1.22	0.2
BH	5.1	3.22	90.72	0.24	0.86	0

Values are percentages of time spent in various postural behaviors for each troop

	CT vs. KK vs. BH	CT vs. KK	CT vs. BH	KK vs. BH
G-Value	30.316	24.35	2.25	17.455
Critical X ² value	7.815 (.05)	5.991 (.05)	5.991 (.05)	5.991 (.05)
Significance	***	***	ns	***

Postural behaviors pooled into three categories; see text for details
 ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

	CT vs. KK	CT vs. BH	KK vs. BH
Sit	ns	*	**
Lie	ns	ns	**
Stand	ns	ns	ns

ANOVAs for different locomotor behaviors

Locomotor behaviors pooled into three categories; see text for details
 ns: not significant

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 20. Percent of time in postural behavior by maintenance activity

	PL	R	S	ST	SS	Other	n
<u>Baobab</u>							
Feed	0.25	0	98.48	1.08	0.25	0	396
Rest	7.08	3.84	88.48	0.6	0	0	833
Social	10.53	23.68	65.79	0	0	0	38
<u>Kaskazi</u>							
Feed	0	0.59	98.22	0.3	0.89	0	337
Rest	8.68	5.79	85.05	0.19	0.29	0	1037
Social	10.39	41.56	46.75	0	0	1.32	77
<u>Colobus Trust</u>							
Feed	0.27	0.53	97.61	0.27	1.33	0	376
Rest	7.77	3.27	88.75	0.1	0.1	0	978
Social	2.86	11.43	85.71	0	0	0	35

Appendix B: Figures

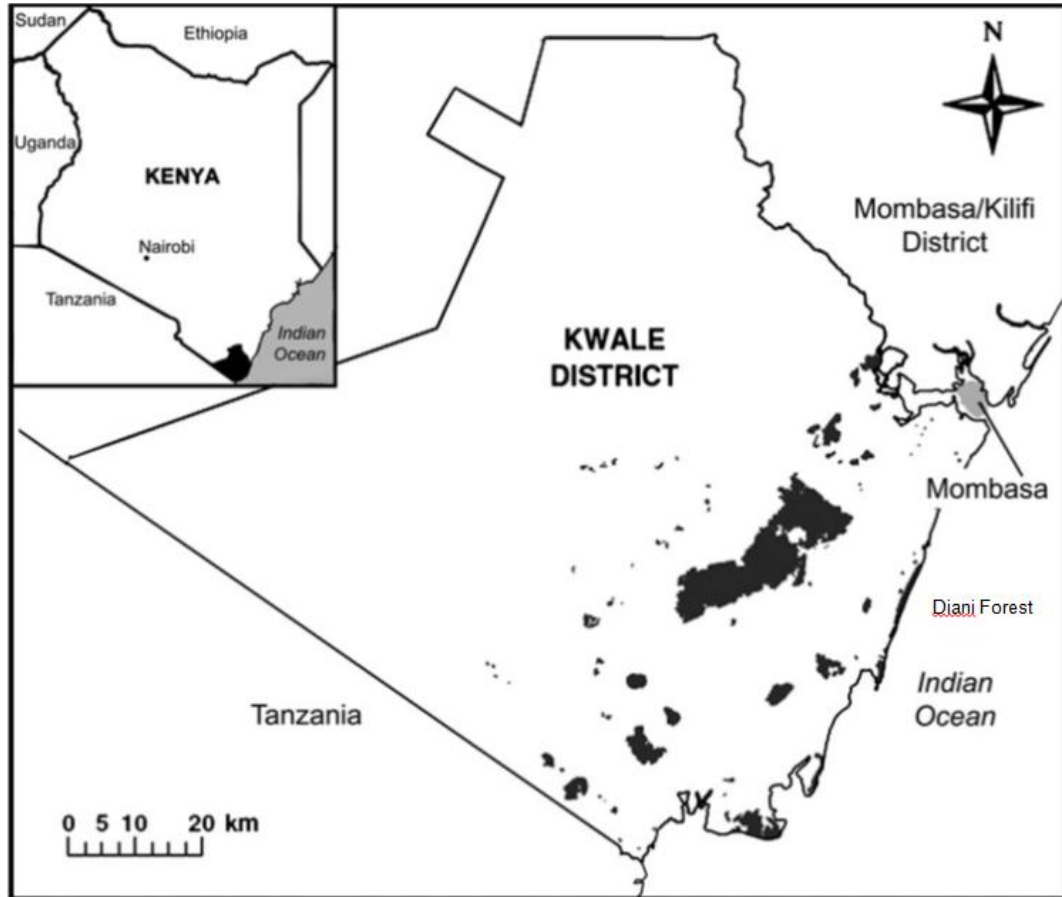


Figure 1. Location of Diani Forest



Figure 2. *Colobus angolensis palliatus*

Drawing courtesy of Steven Nash

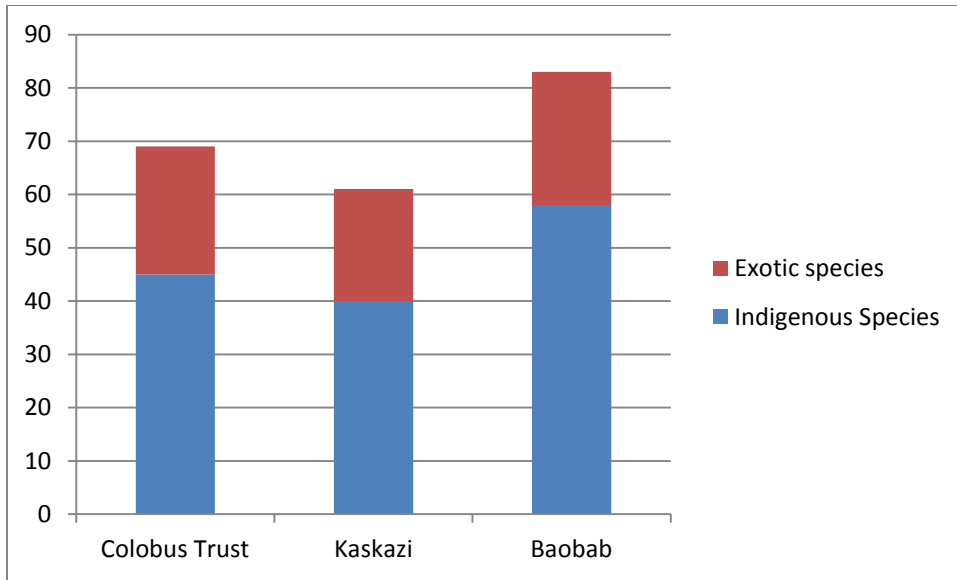


Figure 3. Tree species richness for each forest area

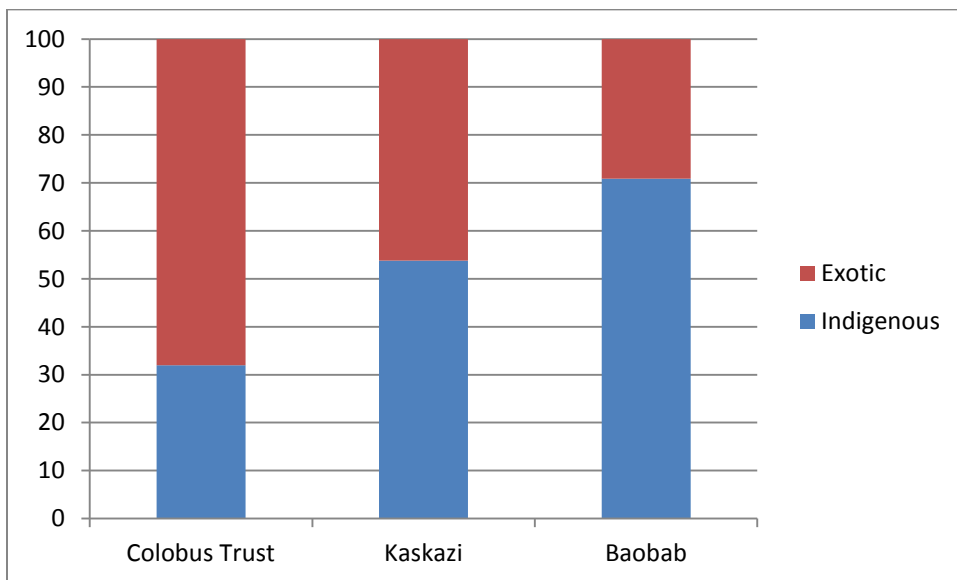


Figure 4. Percent of individual indigenous vs. exotic trees in each forest area

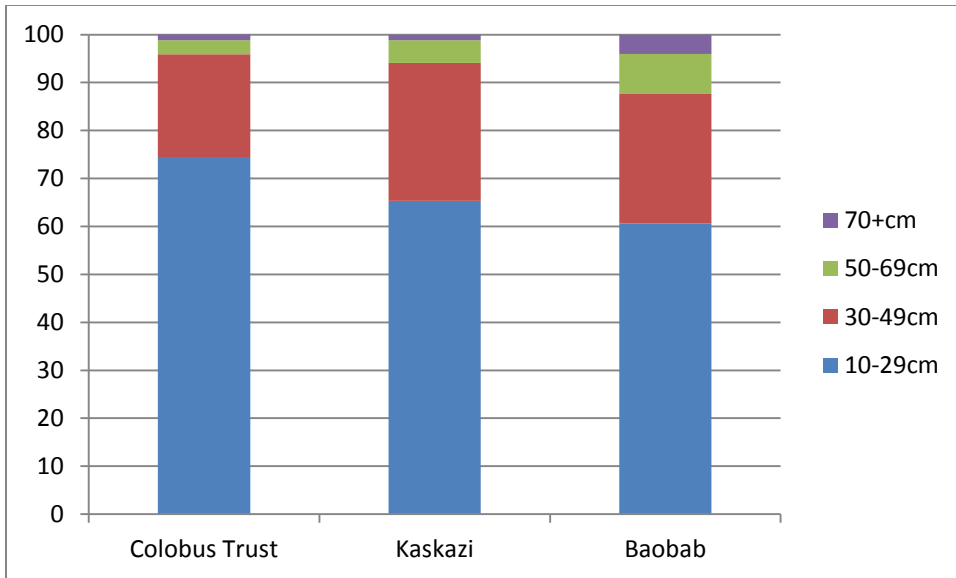


Figure 5. Percent of trees by DBH category for each forest area

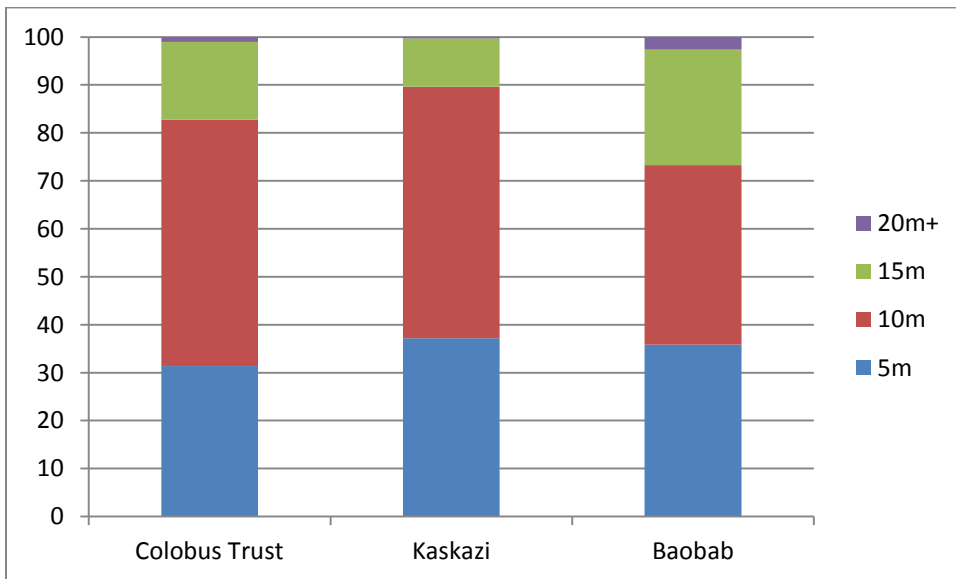


Figure 6. Percent of trees by height category for each forest area

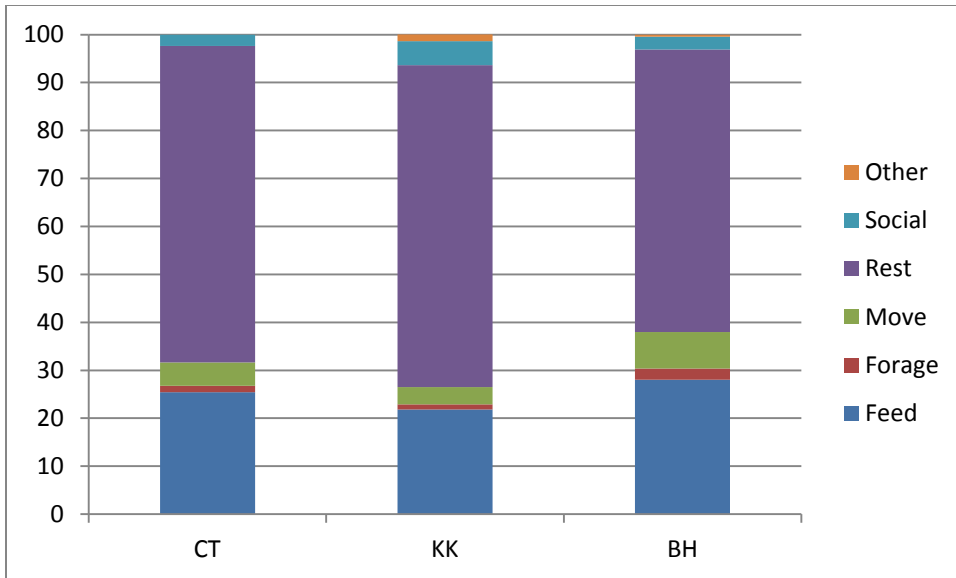


Figure 7. Percent of time in maintenance activities

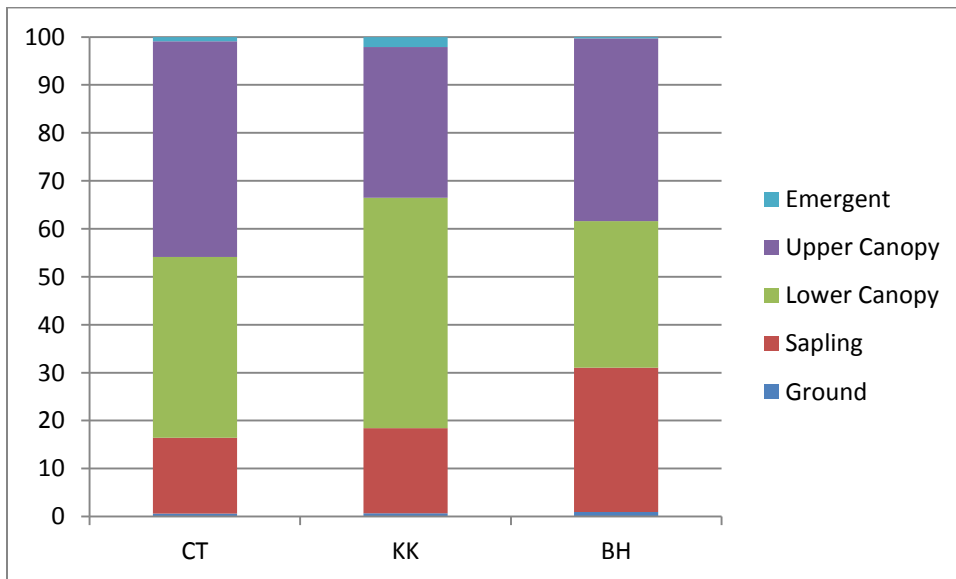


Figure 8. Percent of time at different strata

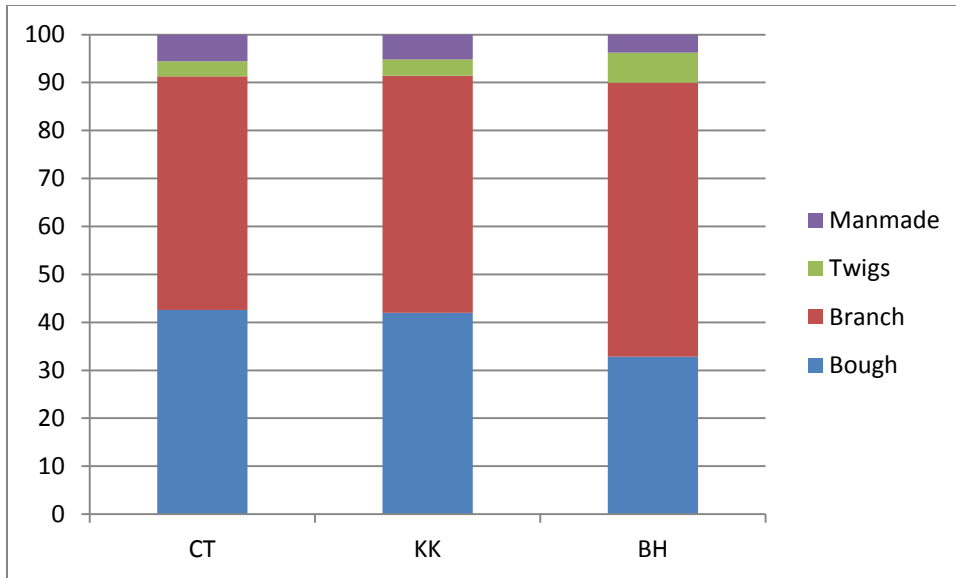


Figure 9. Percent of time on different supports

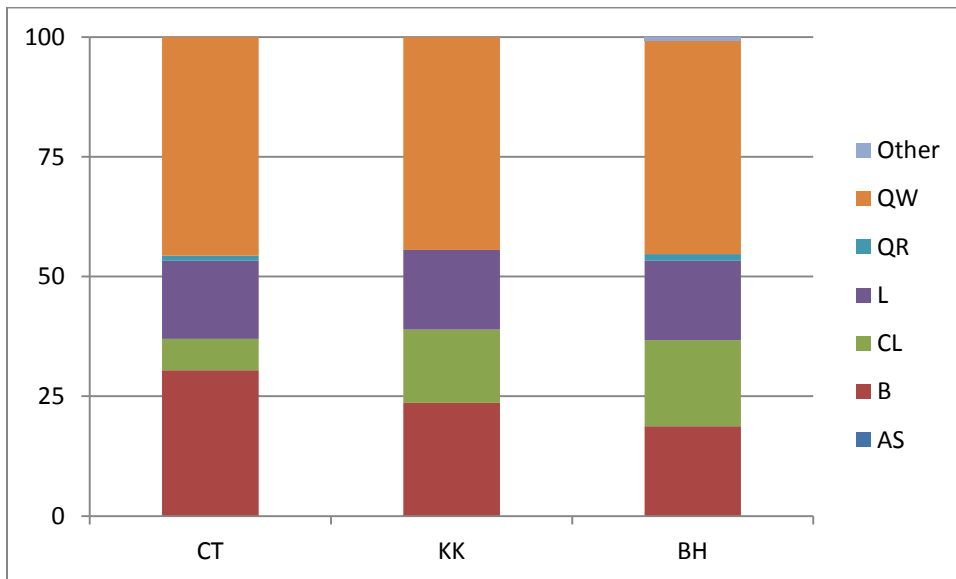


Figure 10. Percent of time in different locomotor behaviors

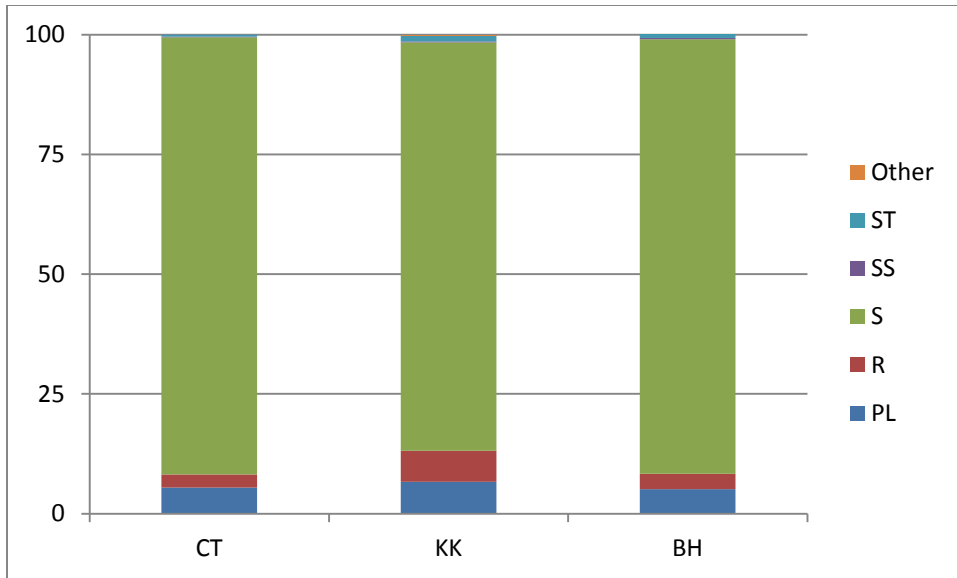


Figure 11. Percent of time in different postural behaviors

Appendix C: Images

All images taken by Noah Dunham



Figure 12. Baobab study area: main canopy



Figure 13. Baobab study area: understory



Figure 14. Baobab study area: hotel portion



Figure 15. Colobus Trust study area: main canopy with frequent gaps



Figure 16. Colobus Trust study area: one of many houses interspersed throughout the area



Figure 17. Kaskazi Study area: main entrance



Figure 18. Kaskazi study area: discontinuous canopy and absence of understory.



Figure 19. Kaskazi study area: maintenance area and trash dump



Figure 20. Black and white colobus sitting dangerously close to poorly insulated power lines



Figure 21. Adult female leaping from branch



Figure 22. Sub-adult walking on hotel balcony



Figure 23. Adult male quadrupedal walking on wall



Figure 24. Two adult females and infant sitting on rooftop

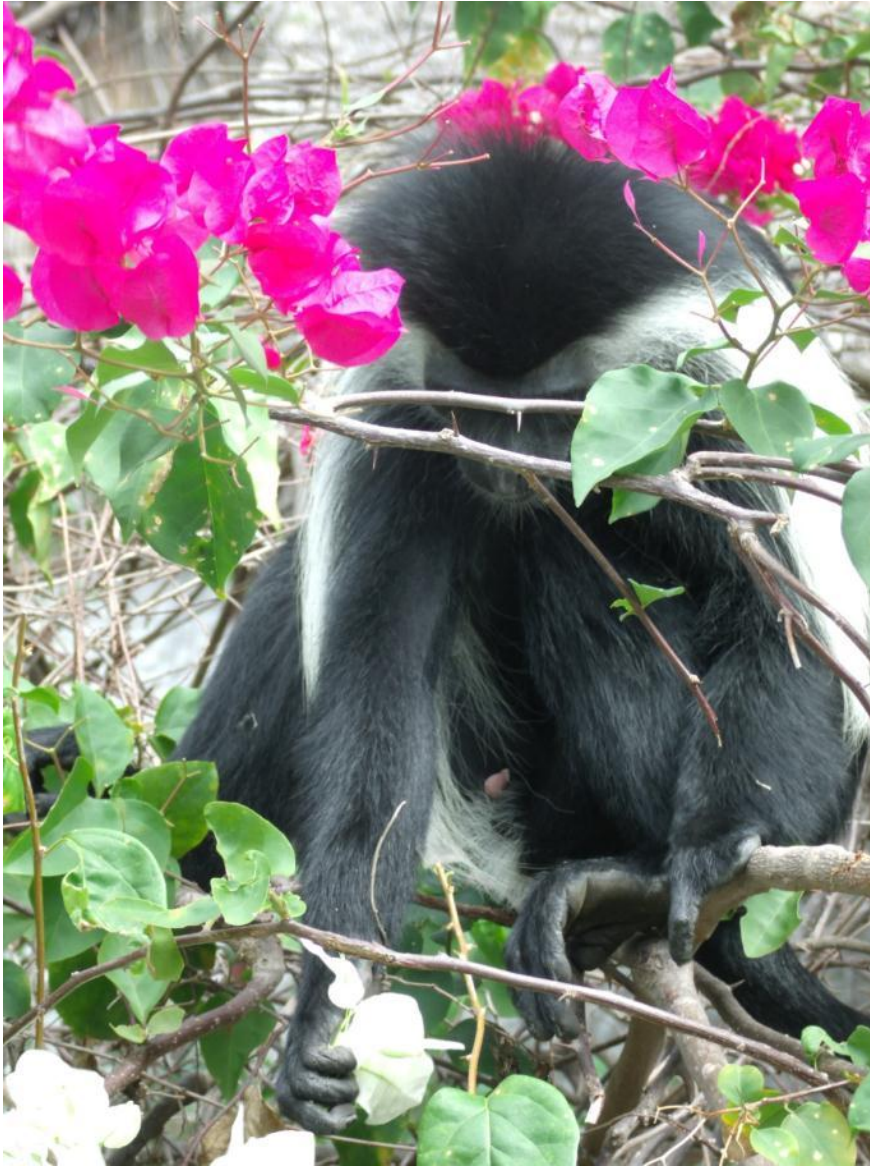


Figure 25. Adult male sitting while feeding on *Bougainvillea spectabilis*

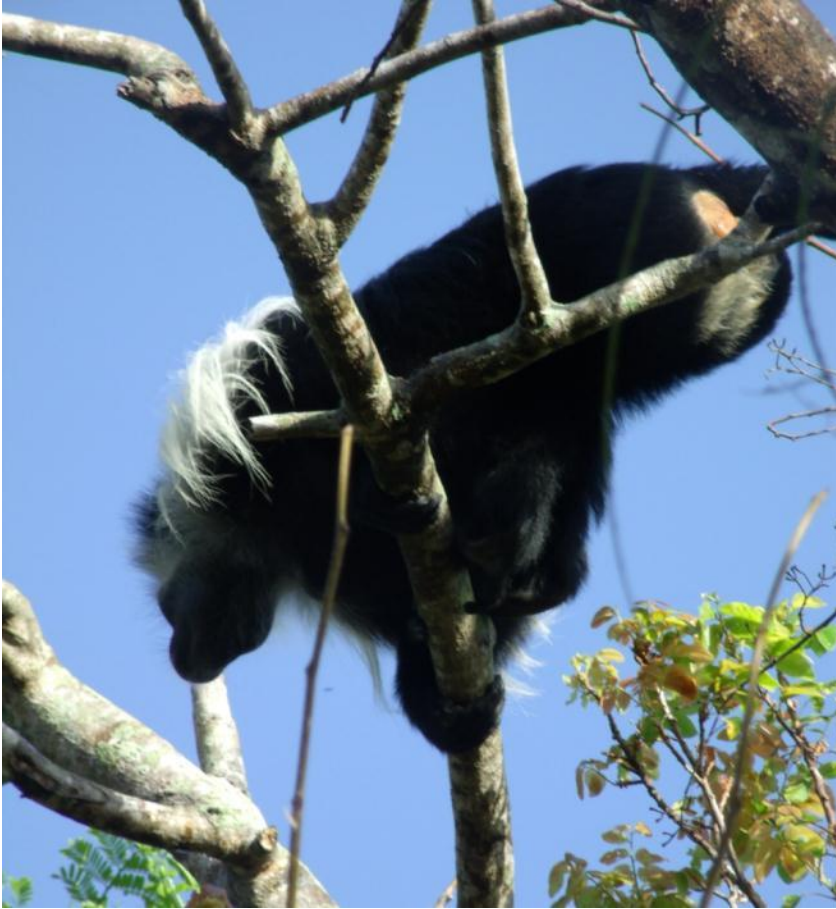


Figure 26. Adult female standing on branch



Figure 27. Adult male prone lying on bough



Figure 28. Sub-adult female grooming a reclining adult female



Figure 29. Adult female and newborn resting in tangled understory



Figure 30. Sub-adult feeding on *Premna hildebrandtii*