

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

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Abstract: We studied the positional behavior and habitat use of adult Peters' Angola black and white colobus monkeys (*Colobus angolensis palliatus*) in the Diani Forest of south coastal Kenya. Data were collected from June-August of 2012 on three groups inhabiting different forest patches characterized by varying levels of degradation. Habitat differences were quantified with regard to tree species composition, tree size, and diversity indices. Results indicate that overall stratum use differed significantly among all groups while support use of one group was significantly different from that of the others. Overall locomotor and postural behaviors were largely consistent among all habitats. Locomotion was comprised predominantly of quadrupedal walking and bounding with fewer instances of climbing and leaping. The most frequently adopted position was sitting, accounting for at least 85% of postural observations for all groups. The dramatic intergroup differences in strata and support use at the Diani site demonstrate that *Colobus* spp. do respond to localized structural conditions; however, that the positional repertoires were consistent across sites provide clear evidence that locomotion and posture are more constrained.

Key words: primate locomotion, posture, support use, strata use, colobus monkeys

INTRODUCTION

Understanding how prosimians, monkeys, and apes move through their environments has been a central aim of primatology since the earliest field studies (Carpenter 1934; Ripley 1967; Walker 1969; Richard 1970; Rose 1974; Fleagle 1976). Primates have evolved an extraordinary array of positional adaptations and knowing when, where and why locomotor and postural behaviors are used in living animals helps illustrate the selective landscape in which postcranial anatomies evolved. Early studies of positional behavior emphasized a categorical approach: species were assigned to locomotor groups based on dominant movements and postures (e.g., quadrupeds, brachiators, and semi-brachiators)

and these behaviors linked to different anatomical complexes (postcranial anatomy) (Erikson 1963; Ashton & Oxnard 1964; Prost 1965; Napier 1967; Ripley 1967; Stern & Oxnard 1973). Most of these categories are still in use (Hunt *et al.* 1996).

Subsequent field workers sought to identify factors that drove intra- and inter-specific variation and to establish behavioral traits associated with a given anatomical complex. Fleagle and Mittermeier (1980) were among the first to explicitly test the extent that positional behaviors varied as a function of body size, activity pattern, substrate use, and forest strata, and multiple studies have since explored how these relationships hold in other primates (Fleagle

1980; Gebo 1987; Cant 1988; Hunt 1992, 1994; Doran 1993; Gebo & Chapman 1995a, 1995b; Remis 1995; McGraw 1998a, 1998b, 2000; Youlatos 1999; Bitty & McGraw 2007). In the course of these studies, a host of other factors that could drive positional differences between individuals, populations, and/or species were identified. These can be sorted into three categories: social (e.g., age, sex, status classes), physiological (e.g., body size, energetic constraints) and environmental (e.g., support availability at different strata, support inclination, canopy height, tree size, liana density, forest type) (Garber 1998, 2011). In addition to demonstrating that behaviors vary and grade into one another, these studies underscore the notion that positional behavior reflects both ultimate (i.e., evolutionary) and proximate (i.e., ecological) influences (Mayr 1961, 1993; Pounds 1991). Given the latter point, one question that has received a good deal of attention is how much behavior varies when proximate (e.g., habitat) conditions change.

The extent that a species' positional repertoire is consistent across structurally different forests is important because it impacts our ability to reconstruct fossil behavior based on living species. Inferences about extinct primates rely on the strength of analogies based on extant taxa (Plavcan *et al.* 2002), so determining the degree that behavior is context-specific is essential. If no modern analogy exists for a trait observed in fossil taxa, behavioral reconstruction is virtually impossible (Kay 1984). Similarly, if positional tendencies are not consistently associated with a particular morphology, or if a species moving in different habitats changes its behavior to degrees not anticipated, then inferences about past behavior may be equally futile. On the other hand, if behavior(s) is reliably associated with a particular anatomy and performance does not significantly change with habitat, then reconstructions of past lifeways from modern models are tenable (Dagosto & Gebo 1998; Garber 1998).

Additional inquiry into the ecological determinants of positional behavior variation is warranted because the diversity of studies to date has yielded contradictory results. In several taxa, positional behavior and support use were conserved across habitat types (Garber & Pruetz 1995; McGraw 1996; Manduell *et al.* 2012) while other taxa exhibited significantly different positional behavior frequencies in structurally distinct forests (Gebo & Chapman 1995b; Dagosto & Yamashita 1998; Schubert 2011). These mixed results are likely due to a combination of factors including challenges

associated with quantifying habitat structures, differences in behavioral sampling methods (i.e., instantaneous vs. continuous sampling), idiosyncrasies in defining positional categories, inter-observer error, and differences in the behavioral flexibility of individual species (Dagosto & Gebo 1998). In this paper, we investigate several of these factors by examining the positional repertoire and habitat use of Peters' Angola black and white colobus monkeys (*Colobus angolensis palliatus*) inhabiting a habitat gradient within Kenya's Diani Forest. The striking structural differences within the forest at this site provide an excellent context for examining the extent that locomotion and posture vary with habitat.

We tested four null hypotheses:

- H1: All groups will spend the majority of their time in the upper forest strata (i.e., main canopy and emergent layer) as has been documented in other black and white colobus monkey species (McGraw 1994, 1998a; Gebo & Chapman 1995a; Schubert 2011).
- H2: Given constraints imposed by their relatively large body size (7.1-8.9 kg), individuals will utilize large supports most frequently for all activities (McGraw 1996; Schubert 2011).
- H3: Locomotor frequencies will not differ significantly across habitat types and arboreal quadrupedalism (i.e., quadrupedal walking and bounding) will be the most common locomotor mode as described in other species of black and white colobus monkeys (Morbeck 1979; Gebo & Chapman 1995a; McGraw 1996; Schubert 2011).
- H4: Postural frequencies will not differ significantly across habitat types and sitting will be the dominant behavior, as documented in prior studies of other black and white colobus monkeys (Mittermeier & Fleagle 1976; Morbeck 1977, 1979; Rose 1979; Gebo & Chapman 1995a; McGraw 1998b; Schubert 2011).

METHODS

Study Site

Kenya's Diani Forest is part of the Zanzibar-Inhambane Floristic Region stretching from Mozambique to Somalia and is recognized as a biodiversity hotspot with numerous endemic flora and fauna (Metcalf *et al.* 2009). The forest is located in the Kwale District of south coastal Kenya (4°15'30", 4°35'30"S and 39°35'00", 39°34'30"E), measures roughly 10 km long by 0.5 km wide (area = 455 ha) and is one of the few remaining patches

of coral rag forest (Anderson *et al.* 2007b; Metcalfe *et al.* 2009) (Figure 1). The climate 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. Annual rainfall averages 744 millimeters (Mwamachi *et al.* 1995), and temperature ranges from 35°C in dry seasons to 28°C in the rainy seasons (Okanga *et al.* 2006). The humidity ranges from 80–100% year round (Okanga *et al.* 2006).

The forest is home to six primate taxa including small-eared galago (*Otolemur garnettii*), Kenya coast galago (*Galagoides cocos*), vervet monkeys (*Chlorocebus aethiops*), Sykes' monkeys (*Cercopithecus albogularis*), yellow baboons (*Papio cynocephalus*), and Peters' Angola colobus. Angola colobus are found in a variety of forest habitats throughout much of Tanzania and the Kwale District of south coastal Kenya. The IUCN considers *C. a. palliatus* of “least



Figure 2. *Colobus angolensis palliatus* feeding on *Premna hildebrandtii*. Photograph by N. Dunham.

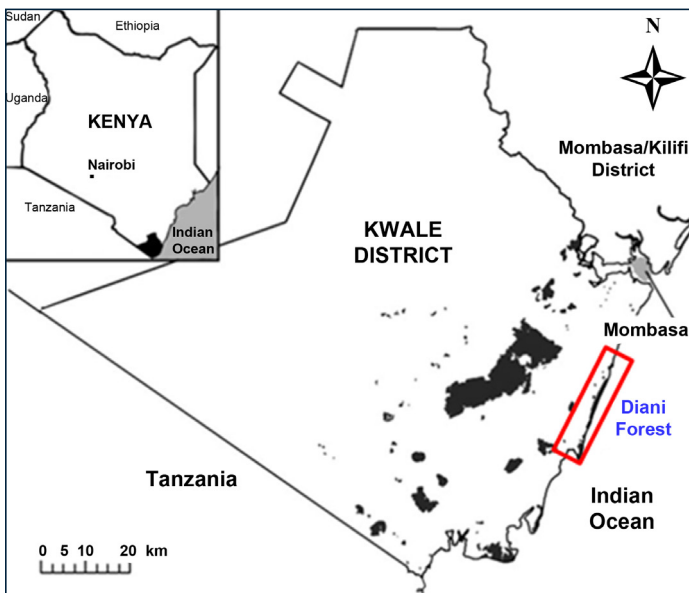


Figure 1. Map of south coastal Kenya forests with location of study site indicated.

concern;” however, in Kenya, the subspecies is considered nationally threatened with likely fewer than 3,000 individuals remaining (Anderson *et al.* 2007b). Recent mitochondrial DNA analyses suggest that *C. a. palliatus* from Kenya and northeastern Tanzania should be considered as a distinct subspecies from the more numerous central Tanzanian forms, highlighting the need for immediate conservation initiatives (McDonald & Hamilton 2010).

Angola colobus are medium sized, sexually dimorphic monkeys: mean body weight for females = 7.1 kg, males = 8.9 kg (Bocian & Anderson 2013) (Figure 2). The few studies conducted on *C. a. palliatus* suggest that they are similar to most other colobines with a predominantly folivorous diet and

energy conservation lifestyle (Lowe & Sturrock 1998; O'Dwyer 2011; Wijtten *et al.* 2012). Like other black and white colobus monkeys, the Angola colobus is highly arboreal and noted for its spectacular leaping ability (Rose 1973, 1979; Moreno-Black & Naples 1977). Groups at Diani average six individuals (range for this study = 5-12) and usually consist of one adult male and multiple adult females and their offspring (Donaldson, pers. comm.). Larger groups of ten or more individuals, including those with two or more adult males, are also present.

Three groups inhabiting ranges within the Diani Forest were examined and labeled Intact Group (IG), Semi-Degraded Group (SDG), and Highly Degraded

Group (HDG). The non-overlapping home ranges of these groups occur in areas representing a gradient from mostly intact forest (IF) dominated by indigenous plant species (Figure 3), to semi-degraded forest (SDF) with residential buildings and exotic plants interspersed throughout (Figure 4), to highly degraded forest (HDF) immediately behind a beach resort (Figure 5). Study group names correspond to forest area names (e.g., the Intact Group (IG) inhabits the Intact Forest (IF) area). To assess differences in forest structure, all trees ($n = 2,341$) greater than 10 cm diameter at breast height (DBH) within each home range area were measured and plotted using a portable GPS device (as in Ganzhorn 2003). We recorded the height (estimated visually in 5 m increments) and DBH of each tree species, classifying each as indigenous or exotic. Overall comparisons of DBH categories and tree height categories using G-tests revealed significant differences among all sites (Table 1).

Positional behavior and support use data were collected from June 10 to August 12, 2012. Each group, fully habituated to human observers prior to this study, was followed on a weekly (4-6 days per week) rotational basis. Data were collected from dawn (6:00) until dusk (18:00). Data were collected on one adult male and two adult females per group. We used an instantaneous time point



Figure 3. Intact forest study area.



Figure 4. Semi-degraded forest study area.



Figure 5. Highly degraded forest study area. All photographs by N. Dunham.

Table 1. Summary of three forest sites in the study area.

Habitat Variables	Forest Site		
	IF ^a	SDF ^b	HDF ^c
Area ^d (ha)	10.49	7.37	5.01
Trees sampled	1145	844	352
Density			
Trees/ha	155.36	114.52	70.26
DBH/ha	3328.18	2758.93	1985.09
Diversity Indices			
Richness	83	69	61
Shannon-Weaver	3.41	2.59	3.34
Evenness	0.77	0.61	0.81
Indigenous Trees (% of sample)	77.1	31.0	59.1
DBH categories (% of sample)			
10-29 cm	59.7	76.2	64.5
30-49 cm	28.5	20.0	29.8
50+ cm	11.9	3.8	5.7
Tree height categories (% of sample)			
5 m	32.0	27.5	36.9
10 m	38.6	56.5	50.9
15+ m	29.4	16.0	12.2

^aIntact Forest; ^bSemi-Degraded Forest; ^cHighly Degraded Forest; ^dHome range size of groups during study period.

sampling scheme at three minute time intervals and did not sample any individual within 15 minutes of itself in order to maintain data independence. The 15 minute time interval is sufficient to avoid temporal auto correlation even among black and white colobus monkeys that spend extended periods resting (C. Janson, personal communication in McGraw 1996). At each time point, we recorded (1) strata (ground, sapling, lower canopy, upper canopy, emergent layer), (2) support type (Table 2), (3) positional behavior (Table 2), and (4) tree species utilized by the focal animal. All categories were used in each habitat; however, because main canopy height differed among the three forest areas, strata categories were recorded independent of substrate height. Differences in the abundance of supports at different strata were readily apparent but were not quantified. A total of 4,134 time point samples were collected over a period of 340 observation hours.

G-tests of interdependence (Sokal & Rohlf 1981) were used to compare overall locomotor and

postural profiles (Doran 1992, 1993; McGraw 1996, 1998a, 1998b). When these tests yielded significant differences, Z-tests were used to compare individual behaviors across positional repertoires (Gerstman 2008). Similarly, overall strata use and support use were compared using G-tests of interdependence and proportions of individual categories were compared using Z-tests. We pooled data on adult males and females within each group after it was determined that the sexes did not differ in any behavior. Statistical tests were performed using SAS 9.3 statistical software.

RESULTS

Strata Use

Overall strata use for each group is shown in Table 3. For all groups, time spent on the ground was less than 1% and time spent in the emergent stratum also constituted a small percentage (0.28-2.1%). The groups were considerably more variable

Table 2. Definitions of positional behaviors and support types.**Locomotor Behaviors^a**

- 1) Quadrupedal Walk: relatively slow, pronograde quadrupedal locomotion
- 2) Quadrupedal Run: faster version of quadrupedal walk, includes diagonal sequence gaits and galloping
- 3) Bound: quadrupedal pronograde locomotion in which the both hindlimbs contact simultaneously followed by both forelimbs contacting simultaneously (usually rapid movement)
- 4) Leap: locomotion with aerial phase between discontinuous supports characterized primarily by hindlimb extension with landing including hindlimbs and/or forelimbs
- 5) Climb: vertical or near vertical (support angle greater than 45°) ascent in which forelimbs reach above head and hind limbs push the animal up
- 6) Arm Swing: locomotion involving forelimb suspension (e.g., brachiation, bimanualism)

Postural Behaviors^a

- 1) Sit: ischia bear a majority of body weight with torso relatively orthograde
- 2) Stand: all four limbs extended on a relatively horizontal support with torso pronograde
- 3) 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
- 4) Prone Lie: lying posture with majority of body weight on the ventral surface; limbs may be dangling below support or tucked under body
- 5) Recline: lying posture with majority of body weight on dorsum or lateral aspect of torso
- 6) Forelimb Suspension: below-support hanging posture using one or more appendages
- 7) Cling: flexed limb posture on relatively vertical support

Support Types^b

- 1) Bough: large supports, greater than 10 cm in diameter and large enough that adult monkeys cannot fully grasp with hands or feet
- 2) Branch: medium-size supports, between 2 and 10 cm in diameter and small enough for adult monkeys to grasp with hand and feet
- 3) Twig: small supports, less than 2 cm in diameter and usually found on the terminal end of branches
- 4) Vertical trunk: vertical support of any diameter in which the monkey must cling
- 5) Artificial support: manmade supports of any size (e.g., rooftop, power line, wall)

^acategories follow Hunt *et al.* 1996; ^ball categories except artificial support follow Mittermeier 1978.

Table 3. Frequencies of strata use, support use, and positional behaviors for three groups of *C. a. palliatus*.

Habitat Use and Positional Behavior Variables	Group		
	IG ^a	SDG ^b	HDG ^c
Strata Use	n = 1413	n = 1480	n = 1544
sapling layer	30.2	15.8	17.8
lower canopy	30.5	37.7	48.0
upper canopy	38.2	45.0	31.5
other	1.2	1.5	2.8
Support Use	n = 1394	n = 1467	n = 1530
bough	32.9	42.6	42.0
branch	57.1	48.7	49.5
twig	6.2	3.1	3.4
artificial	3.8	5.6	5.2
Locomotor Behavior	n = 140	n = 92	n = 72
quad. walk	44.6	45.7	44.4
bound	18.7	30.4	23.6
climb	18.0	6.5	15.3
leap	16.6	16.3	16.7
other	2.1	1.1	0
Postural Behavior	n = 1389	n = 1267	n = 1451
sit	90.7	91.2	85.3
prone lie	5.1	5.5	6.7
recline	3.2	2.8	6.5
stand	1.1	0.6	1.2
other	0	0	0.2

^aIntact Group; ^bSemi-Degraded Group; ^cHighly Degraded Group

in time spent at the sapling level (15.8-30.2%), lower canopy (30.5-48.0%), and upper canopy (31.5-45.0%). Significant differences were present for every comparison of overall strata use ($p < 0.01$ for all pairwise comparisons; Table 4). Similarly, all but one pairwise comparison of individual strata categories yielded significant differences (Table 5). In general, SDG spent more time in the upper canopy, the HDG in the lower canopy, and the IG was nearly even across sapling, lower canopy, and upper canopy strata.

Support Use

Frequencies of support use for each group are reported in Table 3. Comparisons of overall support use revealed no differences for SDG vs. HDG;

however, significant differences were found for IG vs. SDG ($G = 47.6$, $p < 0.01$.) and for IG vs. HDG ($G = 39.7$, $p < 0.01$) (Table 4). The IG utilized boughs significantly less but used branches and twigs significantly more often than SDG and HDG (Table 5).

Locomotor Behavior

Table 3 reports data on locomotor behaviors. Quadrupedal walking was the predominant locomotor mode for all groups (44.4-45.7%), leaping frequencies were nearly identical (16.3-16.7%), but percentages of bounding (18.7-30.4%) and climbing (6.5-18.0%) were more variable. For statistical tests, four locomotor categories were used: quadrupedal walking, bounding, climbing, and

Table 4. Comparison of overall strata use, support use, and positional behavior profiles for three groups of *C. a. palliatus*.

Positional Behavior and Habitat Use Variables	Overall Comparison Using G-Test		
	IG ^a vs. SDG ^b	IG ^a vs. HDG ^c	SDG ^b vs. HDG ^c
Strata Use	G = 85.1, $p < 0.01$	G = 115.2, $p < 0.01$	G = 56.5, $p < 0.01$
Support Use	G = 47.5, $p < 0.01$	G = 39.6, $p < 0.01$	n.s.
Locomotor Behavior	G = 9.2, $p = 0.03$	n.s.	n.s.
Postural Behavior	n.s.	G = 17.5, $p < 0.01$	G = 24.4, $p < 0.01$

^aIntact Group; ^bSemi-Degraded Group; ^cHighly Degraded Group

leaping. Comparisons of overall locomotor profiles revealed no significant differences for IG vs. HDG and SDG vs. HDG, but significant difference for IG vs. SDG ($G = 9.2$, $p = 0.03$; Table 4). Comparisons of individual locomotor behaviors show that the SDG bounded significantly more and climbed significantly less than IG (Table 5).

Postural Behavior

Table 3 reports postural behaviors for each group. Sitting was the most common (85.2-91.2%) posture used by members of each group. Prone lying (5.1-6.7%) and reclining (2.7-6.5%) constituted smaller percentages while quadrupedal standing (0.43-1.2%) and supported standing (0.14-0.24%) were rarely used. For statistical tests, we recognized three categories: sit, prone lie, and recline. Overall postural comparisons yielded non-significant results for IG vs. SDG but significant differences for SDG vs. HDG ($G = 24.4$, $p < 0.01$) and for IG vs. HDG ($G = 17.5$, $p < 0.01$; Table 4). The HDG sat significantly less often and reclined significantly more often than the IG and SDG (Table 5).

DISCUSSION

Due to the extensive variation in structural and ecological characteristics (i.e., tree density, diameter, height, and species composition) across the three forest areas (Table 1), it is no surprise that groups exhibit some significant differences in habitat use. As is common in other black and white colobus species (Davies & Oates 1994) the three groups at Diani spent the majority of time (range = 60.7-82.7%) in the main (upper and lower) canopy. It is possible that members of each group sought high canopy levels as a means of increasing safety: although there are few natural predators, many monkeys at

Diani are killed by domestic dogs and automobiles (Kahumbu 1997). IG, however, spent nearly twice as much time in the sapling layer (30.2%) than either of the other groups (15.8-17.8%), demonstrating that *C. a. palliatus* need not be restricted to a main canopy niche. In the case of IG, we suspect factors such as food availability and support differences at different strata account for this group being found at lower levels. During the study period 50.1% of feeding observations for IG occurred in the sapling layer compared to 35.6% and 33.0% for the SDG and HDG respectively (Dunham, unpublished data).

Overall support use was virtually identical for SDG and HDG, but both differed significantly from IG with the latter utilizing fewer boughs and more branches and twigs. This is almost certainly explicable due to IG's affinity for feeding on *Premna hildebrandtii*, an indigenous plant that grows in tangled clusters on thin supports predominantly in the sapling layer. This plant, which is rare within the SDG and HDG home ranges, constituted the largest portion (28.9%) of the IG's diet compared to less than 1% in the other groups (Dunham, unpublished data). Despite statistically significant differences in support use, all groups spent at least 90% of observations on large (boughs) or medium sized supports (branches) as predicted by constraints associated with large body size.

Inter-group differences in canopy and support use appear to be a function of local habitat features including food availability. Despite these differences, locomotor behaviors are generally consistent across habitats and the few minor differences in individual behaviors are a function of group-specific support preferences (Prost 1965; McGraw 1996, 1998a). Arboreal quadrupedalism (i.e., quadrupedal walking and bounding) comprises between 64 and 76% of each group's locomotor profile followed by similar frequencies of climbing and leaping. No

Table 5. Pairwise comparisons of individual strata use, support use, and positional behavior categories for three groups of *C. a. palliatus*.

Positional Behavior and Habitat Use Variables	Individual Comparison using Z-Test		
	IG ^a vs. SDG ^b	IG ^a vs. HDG ^c	SDG ^b vs. HDG ^c
Strata Use			
sapling layer	Z = 9.2, p < 0.01	Z = 7.9, p < 0.01	n.s.
lower canopy	Z = 4.1, p < 0.01	Z = 9.7, p < 0.01	Z = 5.7, p < 0.01
upper canopy	Z = 3.7, p < 0.01	Z = 3.8, p < 0.01	Z = 7.7, p < 0.01
Support Use			
bough	Z = 5.4, p < 0.01	Z = 5.1, p < 0.01	n.s.
branch	Z = 4.5, p < 0.01	Z = 4.2, p < 0.01	n.a.
twig	Z = 3.9, p < 0.01	Z = 3.6, p < 0.01	n.s.
artificial	Z = 2.3, p = 0.02	n.s.	n.s.
Locomotor Behavior			
quad. walk	n.s.	n.s.	n.s.
bound	Z = 2.1, p = 0.04	n.s.	n.s.
climb	Z = 2.5, p = 0.01	n.s.	n.s.
leap	n.s.	n.s.	n.s.
Postural Behavior			
sit	n.s.	Z = 4.2, p < 0.01	Z = 4.9, p < 0.01
prone lie	n.s.	n.s.	n.s.
recline	n.s.	Z = 3.9, p < 0.01	Z = 4.7, p < 0.01

^aIntact Group; ^bSemi-Degraded Group; ^cHighly Degraded Group

instances of arm swinging or “semi-brachiation” were observed, corroborating results from previous studies (Mittermeier & Fleagle 1976; Morbeck 1977, 1979; McGraw 1996; Schubert 2011). McGraw (1996) argued that one way locomotor modes are conserved across architecturally different habitats is by primates consistently choosing the same support types despite differences in their availability. Support types, in turn, limit the kinds of locomotor behaviors that can be performed. This appears to be the case in the Diani black and white colobus. For example, IG spent more time moving and foraging on small, densely packed clusters of supports that required nimble climbing and quadrupedal walking to navigate. Conversely, SDG engaged in more bounding behavior which is likely facilitated by their greater use of the largest arboreal support type: boughs.

Despite a few statistically significant differences among groups, postural profiles were generally consistent across the three habitats, as predicted. Previous studies have documented the primacy

of sitting behavior (Mittermeier & Fleagle 1976; Morbeck 1977, 1979; Rose 1979; Gebo & Chapman 1995a; McGraw 1998b) and the same was found at Diani with this behavior comprising between 85-91% of all postures for the three groups (Figure 6). After sitting, the three groups followed the same trend in which time spent prone lying > reclining > quadrupedal standing > supported standing.

As noted above, primatologists have long been interested in sources of behavioral variation as well as the extent a primate is able to adjust its behavior to accommodate changes in local ecological conditions. It is clear that there is tremendous variation in the degree to which even closely related species are able to adjust to changing conditions (Struhsaker 2010). Unlike many other cercopithecids including the closely related red colobus monkeys (*Procolobus* spp.), black and white colobus monkeys (*Colobus* spp.) readily adapt to altered forest environments (Fashing 2011). In addition to ranging throughout primary forest, black and white colobus are known to thrive within secondary and degraded forest



Figure 6. A group of *Colobus angolensis palliatus* sitting on a bough in Diani Forest. Photograph by N. Dunham.

fragments where they may be found at densities higher than those reported from primary forests (Onderdonk & Chapman 2000; Anderson *et al.* 2007a, 2007b; Mammides *et al.* 2008). The ability of *Colobus* spp. to not only withstand but thrive in disturbed environments is likely due to their behavioral and dietary flexibility (Marsh 2003). Black and white colobus monkeys are able to use very small home ranges (Fashing 2011) and adapt to food scarcity with an energy conservation strategy of increasing rest while reducing daily travel (Dasilva 1992). The pronounced variation in strata use among the three troops at a single site illustrates the extent that black and white colobus can adjust elements of behavior to suit local conditions.

Still, the remarkable similarity in locomotor and postural behaviors among the *C. a. palliatus* troops inhabiting three structurally distinct forest areas suggests positional behavior is less plastic than other aspects of behavior, most likely due to constraints imposed by musculoskeletal anatomy. That positional behavior is conserved across architecturally different forests has been documented in several species of New and Old World primates (Garber & Pruetz 1995; McGraw 1996; Manduell *et al.* 2012) while other studies have reported significant differences in behavior between distinct forest types (Gebo & Chapman 1995b; Dagosto & Yamashita 1998; Schubert 2011). What factors might account for the apparent inconsistency in results?

First, some investigators argue that minimal differences in locomotor or postural behavior are an artifact of studies that compare forests that are not structurally dissimilar enough to warrant positional behavior differences (McGraw 1996). Although we did not quantify availability of different sized supports as others have done (McGraw 1996; Dagosto & Yamashita 1998; Manduell *et al.* 2012), the striking differences in tree species composition, tree density, DBH and height categories, combined with the significant differences in strata use across the three forest patches, strongly suggest that these habitats differ profoundly in their architecture and that ecological dissimilarity is not an issue.

It is also the case that some taxa are simply more able to adjust their behaviors to different external conditions than are others. In general, red colobus monkeys (*Piliocolobus* spp.) are described as ecologically sensitive monkeys who are less able to adjust their behavior to changing ecology (Struhsaker 2010). Their ecological sensitivity is reflected in the fact that many populations, incapable of adapting to secondary or regenerating forest, are confined to shrinking blocks of undisturbed primary forest. This behavioral inflexibility has been disastrous for the genus: there are no red colobus monkeys in zoos, captive breeding programs have not proven successful, most red colobus species are classified as endangered or critically endangered, and one taxon may have become the first primate in over 400

years to go extinct (McGraw 2005; Oates *et al.* 2001; Struhsaker 2010). In contrast, closely related black and white colobus monkeys are much more able to adjust to habitat perturbation, they are found in a variety of forest types across Africa, and they are quite common in zoological parks (Mittermeier *et al.* 2013; Rowe & Myers 2013). Understanding the basis for this dichotomy has profound conservation implications and we look forward to future studies that examine the physiological, social, and ecological drivers of behavioral variation and, in particular, those studies that can explain why some primates are better able to adjust their behaviors- including positional behavior- than others (Garber 2011).

SUMMARY AND CONCLUSION

We suggest that differences in forest structure and ecological variables among three areas of the Diani Forest account for variation in overall strata use and support use. Locomotor and postural behaviors are largely consistent across habitat types. It is possible that our results are a victim of scale (Chapman *et al.* 2002) and that long term study could yield significantly different positional behavior repertoires (Garber 2011); however, we argue that positional behavior is largely constrained by morphology - regardless of the scale and predict that additional examination of the Diani populations would generate results similar to ours. These findings emphasize the link between morphology and behavior and strengthen our confidence in using morphology to reconstruct the behavior of fossil primates.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2012136655, The Ohio State University, and the Earth and Space Foundation. We recognize the Kenyan government for permission to conduct this research. Special thanks to Andrea Donaldson, Keith Thompson, and Pam Cunneyworth of Colobus Conservation for providing logistical support and advice for this study. We would especially like to thank John Ndege and Bakari Mnyenze for their expertise in plant identification and assistance in data collection. We thank Dr. Barbara Piperata, Erin Kane, and three anonymous reviewers for their comments on earlier versions of this manuscript.

LITERATURE CITED

- Anderson, J., G. Cowlshaw, & J.M. Rowcliffe. 2007a. Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. *International Journal of Primatology* 28(3): 637-655.
- Anderson, J., J.M. Rowcliffe, & G. Cowlshaw. 2007b. The Angola black-and-white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. *American Journal of Primatology* 69(6): 664-680.
- Ashton, E.H. & C.E. Oxnard. 1964. Locomotor patterns in primates. *Proceedings of the Zoological Society of London* 142(1): 1-28.
- Bitty, E.A. & W.S. McGraw. 2007. Locomotion and habitat use of Stampflii's putty-nosed monkey (*Cercopithecus nictitans stampflii*) in the Tai National Park, Ivory Coast. *American Journal of Physical Anthropology* 134(3): 383-391.
- Bocian, C.M. & J. Anderson. 2013. *Colobus angolensis*: Angola colobus (Angola black and white colobus, Angola pied colobus). In *Mammals of Africa: Vol II Primates*, T.M. Butynski, J. Kingdon & J. Kalina eds. Bloomsbury Publishing, London.
- Carpenter, C.R. 1934. A field study of the behavior and social relations of howling monkeys. *Comparative Psychology Monographs* 10(48):1-168.
- Cant, J.G.H. 1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in northern Sumatra. *American Journal of Physical Anthropology* 76(1): 29-37.
- Chapman, C.A., L.J. Chapman, & T.R. Gillespie. 2002. Scale issues in the study of primate foraging: red colobus of Kibale National Park. *American Journal of Physical Anthropology* 117(4): 349-363.
- Dagosto, M. & N. Yamashita. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. *Primates* 39(4): 459-472.
- Dagosto, M. & D.L. Gebo. 1998. Methodological issues in studying positional behavior: meeting Ripley's challenge. In *Primate Locomotion: Recent Advances*. E. Strasser, J. Fleagle, A. Rosenberger & H. McHenry, eds. Plenum Press, New York. Pp. 5-29.
- Dasilva, G.L. 1992. The western black and white colobus as a low energy strategist: activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology* 61(1): 79-91.
- Davies, A.G. & J.F. Oates. 1994. *Colobine Monkeys: Their Ecology, Behavior and Evolution*. Cambridge University Press: Cambridge.

- Doran, D. 1992. Comparison of instantaneous and locomotor bout sampling methods: a case study of adult male chimpanzee locomotor behavior and substrate use. *American Journal of Physical Anthropology* 89(1): 85–99.
- Doran, D. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. *American Journal of Physical Anthropology* 91(1): 99–115.
- Erikson, G.E. 1963. Brachiation in the New World monkeys and anthropoid apes. *Symposium for the Zoological Society of London* 10: 135–164.
- Fashing, P.J. 2011. African colobine monkeys. In *Primates in Perspective*. C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder & R.M. Stumpf, eds. Oxford University Press, Oxford. Pp. 203–229.
- Fleagle, J.G. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatologica* 26(4): 245–269.
- Fleagle, J. G. 1980. Locomotion and posture. In *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest*. D. J. Chivers, ed. Plenum Press, New York. Pp. 191–207.
- Fleagle, J.G. & R.A. Mittermeier. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology* 52: 301–314.
- Ganzhorn, J.U. 2003. Habitat description and phenology. In *Field and Laboratory Methods in Primatology*. M. Setchell & D.J. Curtis eds. Cambridge University Press, Cambridge. Pp. 40–56.
- Garber, P.A. 1998. Within and between site variability in moustached tamarin (*Saguinus mystax*) positional behavior during food procurement. In *Primate Locomotion*. E. Strasser, J. Fleagle, A.L. Rosenberger & H. McHenry, eds. Plenum, New York. Pp. 61–78.
- Garber, P.A. 2011. Primate locomotor positional behavioral and ecology. In *Primates in Perspective*. C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder & R.M. Stumpf, eds. Oxford University Press, Oxford. Pp. 548–563.
- Garber, P.A. & J.D. Pruetz. 1995. Positional behavior in moustached tamarin monkeys: effects of habitat on locomotor variability and locomotor stability. *Journal of Human Evolution* 28(5): 411–426.
- Gebo, D.L. 1987. Locomotor diversity in prosimian primates. *American Journal of Primatology* 13(3): 271–281.
- Gebo, D.L. & C.A. Chapman. 1995a. Positional behavior in five sympatric Old World monkeys. *American Journal of Physical Anthropology* 97(1): 49–76.
- Gebo, D.L. & C.A. Chapman. 1995b. Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. *American Journal of Physical Anthropology* 96(1): 73–82.
- Gerstman, B.B. 2008. *Basic Biostatistics: Statistics for Public Health Practice*. Jones and Bartlett Publishers, Sudbury, Mass.
- Hunt, K. D. 1992. Positional behavior of Pan troglodytes in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology* 87(1): 83–105.
- Hunt, K.D. 1994. Body size effects on vertical climbing among chimpanzees. *International Journal of Primatology* 15(6): 855–865.
- Hunt, K.D., J. Cant, D. Gebo, M. Rose, S. Walker & D. Youlatos. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* 37(4): 363–387.
- Kay, R.F. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys and Apes*. P.S. Rodman & J.G.H. Cant, eds. Columbia University Press, New York. Pp. 21–53.
- Kahumbu, P. 1997. The decline of the Angolan colobus monkeys (*Colobus angolensis palliatus*) in Diani. *Journal of the East African Natural History Society* 27: 2–3.
- Lowe, A.J. & G.A. Sturrock. 1998. Behaviour and diet of *Colobus angolensis palliatus* Peters 1868, in relation to seasonality in a Tanzanian dry coastal forest. *Folia Primatologica* 69(3): 121–128.
- Mammides, C., M. Cords & M.K. Peters. 2008. Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. *African Journal of Ecology* 47(1): 87–96.
- Manduell, K.L., M.E. Harrison & S.K.S. Thorpe. 2012. Forest structure and support availability influence orangutan locomotion in Sumatra and Borneo. *American Journal of Primatology* 74(12): 1128–1142.
- Marsh, L. 2003. The nature of fragmentation. In *Primates in Fragments: Ecology and Conservation*. L.K. Marsh, ed. Kluwer Academic, New York. Pp. 1–10.
- Mayr, E. 1961. Cause and effect in biology. *Science* 131(3489): 1501–1506.
- Mayr, E. 1993. Proximate and ultimate causation. *Biology and Philosophy* 8(1): 95–98.
- McDonald, M.M. & H. Hamilton. 2010.

- Phylogeography of the Angolan black and white colobus monkey, *Colobus angolensis palliatus*, in Kenya and Tanzania. *American Journal of Primatology* 72(8): 715-724.
- McGraw, W.S. 1994. Census, habitat preference, and polyspecific associations of six monkeys in the Lomako Forest, Zaire. *American Journal of Primatology* 34(4): 295-307.
- McGraw, W.S. 1996. Cercopithecoid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 100(4): 507-52.
- McGraw, W.S. 1998a. Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 105(4): 493-510.
- McGraw, W.S. 1998b. Posture and support use of Old World monkeys (Cercopithecidae): the influence of foraging strategies, activity patterns and the spatial distribution of preferred food items. *American Journal of Primatology* 46(3): 229-250.
- McGraw, W.S. 2000. Positional behavior of *Cercopithecus petaurista*. *International Journal of Primatology* 21(1): 151-182.
- McGraw, W.S. 2005. Update on the search for Miss Waldron's red colobus monkey. *International Journal of Primatology* 26(3): 605-619.
- Metcalfe, K., R. French-Constant & I. Gordon. 2009. Sacred sites as hotspots for biodiversity: the three sisters cave complex in coastal Kenya. *Oryx* 44(1): 118-123.
- Mittermeier, R.A. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatologica* 30(3): 161-193.
- Mittermeier, R.A. & J.G. Fleagle. 1976. The Locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. *American Journal of Physical Anthropology* 45(2): 235-256.
- Mittermeier, R.A., A.B. Rylands & D.E. Wilson. 2013. *Handbook of the Mammals of the World: Vol III Primates*. Lynx Edicions, Barcelona.
- Morbeck, M.E. 1977. Positional behavior, selective use of habitat substrate and associated non-positional behavior in free-ranging *Colobus guereza*. *Primates* 18(1): 35-58.
- Morbeck, M.E. 1979. Forelimb use and positional adaptation in *Colobus guereza*: integration of behavioral, ecological, and anatomical data. In *Environment, Behavior and Morphology: Dynamic Interactions in Primates*. M.E. Morbeck, H. Preuschoft & N. Gomberg, eds. Gustav Fischer, New York. Pp. 95-117.
- Moreno-Black, G. & W.R. Naples. 1977. Differential habitat utilization of four Cercopithecidae in a Kenyan forest. *Folia Primatologica* 27(2): 85-107.
- Mwamachi, D.M., J.O. Audho, W. Thorpe & R.L. Baker. 1995. Evidence for multiple anthelmintic resistance in sheep and goats reared under the same management in coastal Kenya. *Veterinary Parasitology* 60(3-4): 303-313.
- Napier, J.R. 1967. Evolutionary aspects of primate locomotion. *American Journal of Physical Anthropology* 27(3): 333-342.
- Oates, J.F., M. Abedi-Lartey, W.S. McGraw, T.T. Struhsaker & G.H. Whitesides. 2001. Extinction of a West African red colobus monkey. *Conservation Biology* 14(5): 1526-1532.
- Onderdonk, D.A. & C.A. Chapman. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology* 21(4): 587-611.
- Okanga, S., G. Muchemi, N. Maingi, E. Mogoa & E. Munene. 2006. Gastrointestinal parasite of free-ranging colobus monkeys (*Colobus angolensis palliatus*) in Kwale District, Kenya coast. *African Journal of Ecology* 44(3): 410-412.
- O'Dwyer, R. 2011. The black-and-white-colobus monkeys (*Colobus angolensis palliatus*) of Diani Forest, Kenya: Behavioural responses to habitat fragmentation. MSc thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Plavcan, J.M., R.F. Kay, W.L. Jungers & C.P. van Schaik. 2002. *Reconstructing behavior in the primate fossil record*. New York: Kluwer Academic/Plenum.
- Pounds, J.A. 1991. Habitat structure and morphological patterns in arboreal vertebrates. In *Habitat Structure: The Physical Arrangement of Objects in Space*. S. Bell, E. McCoy & H. Mushinsky eds. Chapman and Hall, New York. Pp. 109-119.
- Prost, J.H. 1965. A definitional system for the classification of primate locomotion. *American Anthropologist* 67(5): 1198-1214.
- Richard, A.F. 1970. A comparative study of the activity patterns and behavior of *Allouata villosa* and *Ateles geoffroyi*. *Folia Primatologica* 12(4): 241-263.
- Ripley, S. 1967. The leaping of langurs: a problem in the study of locomotor adaptation. *American Journal of Physical Anthropology* 26: 149-170.
- Remis, M. 1995. Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology* 97(4): 413-433.

- Rose, M.D. 1973. Quadrupedalism in primates. *Primates* 14(4): 337–357.
- Rose, M.D. 1974. Postural adaptations in New and Old World monkeys. In *Primate Locomotion*. F.A. Jenkins, eds. Academic Press, New York. Pp. 201–222.
- Rose, M.D. 1979. Positional behavior of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*. M.E. Morbeck, ed. Gustav Fisher, New York. Pp. 75–93.
- Rowe, N. & M. Myers. (eds). 2013. www.alltheworldsprimates.org. Charlestown, RI: Primate Conservation Inc.
- Schubert, R.L. 2011. 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. PhD dissertation, The Ohio State University, Columbus, OH, USA.
- Sokal, R.R. & F.J. Rohlf. 1981. *Biometry: The Principles and Practice of Statistics in Biological Research*. WH Freeman and Company, New York.
- Stern J.T & C.E. Oxnard. 1973. Primate locomotion: some links with evolution and morphology. *Primates* 4: 1–93.
- Struhsaker, T.T. 2010. *The Red Colobus Monkeys: Variation in Demography, Behavior, and Ecology of Endangered Species*. Oxford University Press, Oxford.
- Walker, A. 1969. The locomotion of the lorises, with special reference to the potto. *East African Wildlife Journal* 7: 1–5.
- Wijten, Z., E. Hankinson, T. Pellissier, M. Nuttall & R. Lemarkat. 2012. Activity budgets of Angola black and white colobus (*Colobus angolensis palliatus*) in an East African coastal forest. *African Primates* 7(2): 203–210.
- Youlatos, D. 1999. Comparative locomotion of six sympatric primates in Ecuador. *Annales des Sciences Naturelles* 20(4): 161–168.

Received: 3 April 2014

Accepted: 24 May 2014