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Activity Budgets of Peters' Angola Black-and-White Colobus (*Colobus angolensis palliatus*) in an East African Coastal Forest

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Abstract: Activity budgets of primates are commonly associated with strategies of energy conservation and are affected by a range of variables. In order to establish a solid basis for studies of colobine monkey food preference, food availability, group size, competition and movement, and also to aid conservation efforts, we studied activity of individuals from social groups of *Colobus angolensis palliatus* in a coastal forest patch in southeastern Kenya. Our observations (N = 461 hours) were conducted year-round, over a period of three years. In our *Colobus angolensis palliatus* study population, there was a relatively low mean group size of 5.6 ± SD 2.7. Resting, feeding, moving and socializing took up 64%, 22%, 3% and 4% of their time, respectively. In the dry season, as opposed to the wet season, the colobus increased the time they spent feeding, traveling, and being alert, and decreased the time they spent resting. General activity levels and group sizes are low compared to those for other populations of *Colobus* spp. We suggest that Peters' Angola black-and-white colobus often live (including at our study site) under low preferred-food availability conditions and, as a result, are adapted to lower activity levels. With East African coastal forest declining rapidly, comparative studies focusing on *C. a. palliatus* feeding ecology, dietary flexibility and behavioral plasticity will be essential for in-situ conservation of the species.

Keywords: activity budget, behavior, coastal forest, *Colobus angolensis palliatus*, black-and-white colobus

Résumé: *Les budgets d'activité des primates sont souvent associés à des stratégies de conservation de l'énergie et sont influencés par une gamme de variables. Afin d'établir des bases solides pour des études sur les préférences alimentaires, la disponibilité de nourriture, la taille des groupes, la compétition et les mouvements et aussi afin de contribuer aux efforts de conservation, nous avons étudié l'activité d'individus dans des groupes de* Colobus angolensis palliates *dans un lambeau de forêt côtière dans le Sud-Est du Kenya. Nos observations (N=461 heures) se sont réparties sur toute l'année et ce pendant trois ans. La taille moyenne des groupes de notre population de* Colobus angolensis palliatus *était relativement basse avec 5,6 ± SD 2,7 individus. Le repos, l'alimentation, les déplacements et les interactions sociales prenaient respectivement 64%, 22%, 3% et 4% du temps. En saison sèche, par rapport à la saison des pluies, les colobus augmentaient le temps accordé à l'alimentation, aux déplacements et à l'état d'alerte et réduisaient le temps de repos. Le niveau général d'activité et la taille des groupes sont plus bas que dans d'autres populations de* Colobus spp. *Nous suggérons que les Peters' Colobe noir-et-blanc d'Angola vivent souvent, y inclus dans notre site d'étude, dans des conditions de faible disponibilité de nourriture préférée et, en conséquence, se sont adaptés à de plus faibles niveau d'activité. Dans un contexte de diminution rapide des superficies de la forêt côtière Est-Africaine, des études comparatives se focalisant sur l'écologie alimentaire, la flexibilité alimentaire et la plasticité dans le comportement de* C. a. palliatus *seront essentiels pour la conservation* in-situ *de l'espèce.*

Mots clé: *budgets d'activité, comportement, forêt côtière,* Colobus angolensis palliatus*, colobe noir-et-blanc*

INTRODUCTION

Activity budgets of primates are commonly associated with strategies of energy conservation (Milton, 1998; Oates, 1977; Stanford, 1991; Dasilva, 1992, 1993) and are affected by predator or human pressure; social structure; season; or availability, distribution and quality of food resources (Clutton-Brock, 1975; Milton, 1980; Bennett, 1986; Boinski, 1987; Zhang, 1995; Olupot *et al.*, 1997; Watts, 1998; Kinnaird & O'Brien, 2000).

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Although activity budgets of all five species of black-and-white colobus monkeys have been studied in detail [*Colobus angolensis* (Bocian, 1997), *Colobus guereza* (Oates, 1977; Fashing 2001), *Colobus polykomos* (Dasilva, 1992), *Colobus santanas* (McKey, 1978), *Colobus vellerosus* (Teichroeb *et al.*, 2003)], activity budgets for only one Angolan black-and-white *Colobus* subspecies, *Colobus angolensis ruwenzorii*, have been described (Bocian 1997; Fashing *et al.*, 2007). Distinct changes in diet and behavior have been observed due to seasonal change related to rainfall in *C. polykomos* (Dasilva, 1989, 1992) and due to habitat quality in *C. angolensis*, *C. badius, C. santanas* and *C. guereza* (McKey, 1978; Maisels, 1994). Notes on feeding and behavior, but not activity budgets, in *C. angolensis* have been recorded by Groves (1973), in the Usambara Mountains, northeastern Tanzania.

With the exception of several unpublished reports (Preston, 2002; Fox, 2004; Heinen, 2006; Olsen, 2007; Dunham, 2009), our study is the first to describe the activity budget of Peters's Angola black-and-white Colobus (*Colobus angolensis palliatus* Peters 1868). *Colobus angolensis palliatus* has been described as preferring primary forest (Bocian, 1997), and showing little variation in space-use, which would be expected for species feeding primarily on foliage (Moreno-Black & Maples, 1977). More recent unpublished reports, however, describe a diverse diet consisting as much of fruit and seeds as of leaves (Jansson, 2011).

Colobus angolensis palliatus inhabits the now scarce patches of coastal forest in southern Kenya and Tanzania, where group sizes seem to be unusually small for *Colobus* (Anderson, 2005; Anderson *et al.*, 2006, 2007a, 2007b). The ecological-constraints model proposes that increases in group size lead to increases in within-group feeding competition, necessitating increased travel and, consequently, constraining group size (Milton, 1984; Chapman *et al.*, 1995). Low group size, hence, may be at times a crude indicator of high competition induced by low food availability or habitat suitability (Fimbel *et al.*, 2001; Teichroeb *et al.*, 2003). Lower preference for leaves may indicate lower nutritional value of leaves, or increased availability of other, higher nutrition foods (McKey *et al.*, 1982; Harrison, 1986; Maisels *et al.*, 1994). In addition, in some forests, preferred feeding trees may be targeted for removal (Githitho, 2004; Anderson, 2005), thereby forcing a change in diet. Dietary diversity and the ability to alter behavior to cope with increasing food scarcity over time are characteristics that are likely to contribute to a primate's ability to persist in fragmented forest (Silver & Marsh, 2003; Wasserman & Chapman, 2003; Isabirye-Basuta & Lwanga, 2008).

In order to provide preliminary data on which future research on Angola black-and-white colobus can build, we report on overall and seasonal activity budgets of individuals from over 20 groups of *Colobus angolensis palliatus* in a coastal forest patch in southeastern Kenya. We also briefly suggest further directions for research on *Colobus angolensis palliatus*.

METHODS

We conducted our study in 2.2 km^2 of coral rag forest (Clarke, 2000), locally known as *Mbuyu Tundu* (04°64'60.0"S, 39°38'20.0"E). Human presence at the time of study was limited, but increasing, and the forest's resources have been used by people for centuries. The climate is characterized by a long (April-July) and a short (October-November) wet season, and annual rainfall has a mean of 1020 mm ± SD 190, with a range of 910-1310 mm, as measured between 1998 and 2002. The mean annual temperature is 26°C, with highest mean temperatures of 33°C between November and April (Anderson, 2007a).

The forest is dense and required creating trails for access. We established east-west straight line transects spaced at 200 m intervals, divided into 50 m sections (adapted from Lacher, 2005). A total of 461 hours of *Colobus angolensis palliatus* activity was recorded between February 2007 and August 2010. All behavior was recorded in daylight between 05:20 h and 18:50 h, using a continuous sampling protocol on selected focal individuals. The individuals were not actively habituated; therefore, in an attempt to not affect behavior by our presence, we observed individuals with binoculars from a distance of at least 50 m, and 10 minutes of no visual contact with observers were required before the start of recording. Furthermore, we recorded staring at humans and excluded this behavior from analysis in an attempt to compensate for possible bias induced by human presence. Sleeping, resting, feeding, traveling, staring at humans, alert, active grooming, passive grooming, self-grooming, asocial playing, social playing, territorial display, stiff legs display, fighting, and copulating were recorded as activity states, with durations recorded in minutes and seconds. In addition, group demographics, group canopy position and weather variables were noted. Every 10 minutes, primary group activity was documented by taking an instantaneous scan sample which recorded behavior of >50% of the group (from Altmann, 1974).

For analysis, the year was divided into a wet period (from April to July, and from October to November) and an equally long dry period (from December to March, and

August to September). The calculated group size is the mean of the group counts for all 545 instances in which behavior was recorded for any group in the study area. Sightings of solitary individuals were excluded from this analysis. This method was corroborated by the calculation of group size using the mean of the results from 12 quarterly distance sampling surveys, performed as described by Anderson (2005) over 8950 m of straight line transects. A half-normal function with cosine series expansion was selected according to Akaike's information criteria (AIC) in DISTANCE 6.0 Release 2 (Thomas, 2010). All other tests were done using SPSS (SPSS, 2008). Significance was determined at a probability level of 0.05.

RESULTS

Mean group size derived from our behavioral study was 5.6 ± SD 2.7 (ranging from 1-14 individuals), while mean group size using the distance sampling method was 5.2 ± SD 2.3.

Percentage distribution across activities is presented in Figure 1. Temporal differences in state duration were expressed in terms of both months and season type (Table 1; Figure 2), and analyzed accounting for weather conditions (Figure 2). The time spent in alert state (Pearson: $\chi 2 = 0.649$, n = 255, p = 0.02) and time spent in active grooming state (ANOVA: F = 1.773, df = 242, p = 0.03; and Pearson: $\chi 2 = 0.640$, n = 12, p = 0.03) decreased with the wet season, mainly at the cost of resting.

Sexual differences in behavior were found for feeding activity; males spent 23% and females 18% of their time feeding (t-test: p = 0.05, df = 608). Males spent 52% and females 59% of their time resting, also significantly different (t-test: p = 0.02, df = 608). There were no differences in travelling activity, but females did spend more time grooming, both in active grooming (t-test: p = 0.011, df = 608; male 0.58%, female 2.18%), and passive grooming (t-test: p = 0.003, df = 608; male 0.31%, female 1.96%).

Group size and activity budget data for *C. a. palliatus* at the site of East Segara Forest in Tanzania, and for studies of *C. a. ruwenzorii* in Rwanda and DRC, are presented in Table 2 for comparative purposes.

DISCUSSION

Our results are a product of observations on many groups and individuals over several years and seasons. This study might, therefore, give a broad-based indication of activity budgets, specific for this type of coastal forest, which is relatively dry, small and experiences high levels of resource extraction, common on the coastal or lowland parts of the range of *Colobus angolensis palliatus*.

Continuous sampling methods are known to slightly underestimate traveling and movement, since the activity itself might cause the animal to move out of sight, interrupting the recording of the activity (Rose, 1999). Resting, feeding and staring account for most of the variability in the data. Staring is associated with human presence; the variability in resting and feeding activity does, however, justify discussion of these activities.

Several unpublished studies from the more inland East Sagara Forest in Tanzania (Preston, 2002; Fox, 2004; Heinen, 2006; Olsen, 2007; Dunham, 2009) report activity budgets that are very similar, with the exception of time

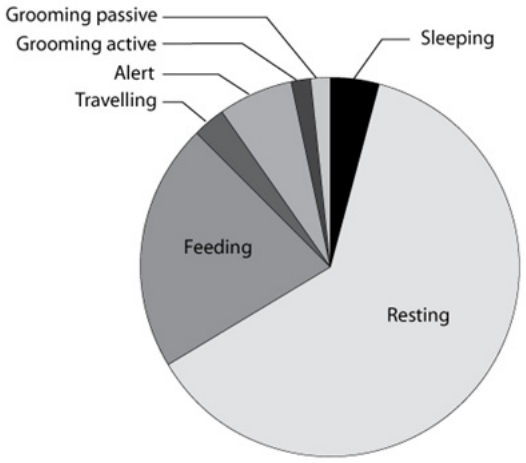

Figure 1. Activity budgets for all recorded activity (N=461 hours): Feeding 21%, Resting 62%, Alert 6%, Sleeping 4%, Travelling 3%, Active grooming 2%, Passive grooming 2%, Sum of other behaviors 4%.

Table 1 - Variation in realtive duration by month of activity state.

State	ANOVA (df=11)
Alert	F = 5.4, P < 0.01
Feeding	F = 3.2, P < 0.01
Resting	F = 6.6, P < 0.01
Staring	F = 13.0, P < 0.01
Travelling	F = 2.2, P = 0.01

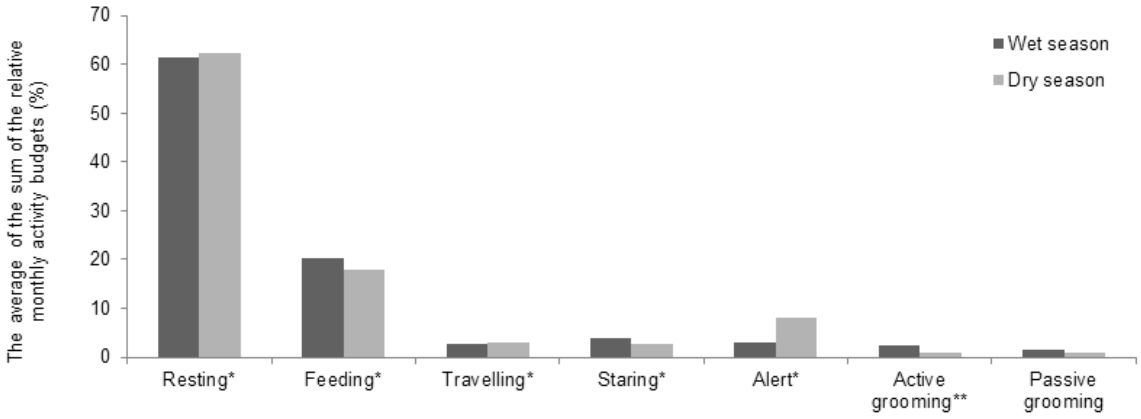

Figure 2. Comparison of the mean of the sum of the relative monthly activity budgets in wet and dry season months. * is indicating a significance level of p ≤ 0.05; ** indicates a significance level of P ≤ 0.1.

Table 2 - Summary of activity budgets reported for *Colobus angolensis* subspecies by research sites. * Indicates were taken from Dunham (2009); Olsen, Heinen, Fox, and Preston and Dunham are unpublished reports.

		Group size	Rest	Feed	Move	Social	Other	
Species	**Study site**	**(mean)**	**(%)**	**(%)**	**(%)**	**(%)**	**(%)**	**References**
C. a. palliatus	Shimoni, Kenya	5.6	64	22	3	4	7	This Study
C. a. palliatus	East Sagara, Tanzania	-	68	14	10	-	-	Olsen (2007)*
C. a. palliatus	East Sagara, Tanzania	-	69	15	8	-	-	Heinen (2006)*
C. a. palliatus	East Sagara, Tanzania	-	69	16	9	-	-	Dunham (2009)*
C. a. palliatus	East Sagara, Tanzania	-	58	21	10	-	-	Fox (2004)*
C. a. palliatus	East Sagara, Tanzania	-	51	29	13	-	-	Preston (2002)*
C. a. ruwenzorii	Nyungwe, Rwanda	> 300	32	42	20	5	1	Fashing et al. (2007a)
C. a. ruwenzorii	Ituri, D.R. Congo	14	43	27	24	5	1	Bocian (1997)

spent moving, which seems to be consistently lower in this study. The more inland *C. a. ruwenzorii* subspecies seems to spend much more time feeding and travelling, and rests nearly half as much as *C. a. palliatus* (see Table 2).

Increased resting levels among colobine monkeys have been linked to vegetation quality (Marsh, 1981). As forest fragments are encroached upon or occupied by humans, typical primate food tree species may become scarce due to logging, clearance for agriculture, changes in micro-climate associated with edge effects, and competition with non-indigenous species (Isabirye-Basuta & Lwanga, 2008). In times of preferred food scarcity, *C. angolensis* often rely heavily on mature leaves, with higher toxin levels, as fallback foods, more so than any other African colobines (Fashing, 2007a). The unique foregut anatomy of *Colobus* allows for fatty acid fermentation, which is believed to be an adaptation to reduce leaf toxin levels prior to absorption (Oates, 1977). An increase in resting activity thus may be explained by the induced need to reduce toxin levels (Dasilva, 1992). Most groups of *C. a. palliatus*, however, seem to incorporate high levels of flowers, fruits, seeds, lianas, lichens, and occasionally, insects into their diets, as well (Fashing, 2007a; unpubl. obs.). This is not uncommon for *Colobus* spp. (Clutton-Brock, 1975; Dunbar, 1987), but is peculiar for a species with numerous adaptations geared towards leaf consumption, and would be inconsistent with the toxin level hypothesis as explanatory for their activity patterns.

Low activity levels among the colobus in our study also could be a result of behavioral adjustment to reduced food availability. Wasserman & Chapman (2003) found that *Colobus guereza* in disturbed areas were less active than those in undisturbed areas, and used that result to propose that colobus in low food availability conditions can lower their activity levels to conserve energy. If their hypothesis is correct, feeding and travelling activity might be expected to increase in periods of higher food abundance. Differences in activity over the year should support this hypothesis. In this view, colobus should minimize activity in periods of low food availability in order to conserve energy, and it might be a factor in the increase in resting and decrease in feeding behavior during the dry season. In our study, however, travelling actually increased in the wet season. More importantly, no data have yet been collected on seasonal food availability at our site, and it is likely that food availability is higher, instead of lower, just after the wet seasons.

The mean group size for *Colobus angolensis palliatus* in Kenya (5.6 ± SD 2.7, this study; 5.6 ± SE 0.2, Anderson, 2007) is unusually low for colobines in Africa. The ecological-constraints model proposes that larger group sizes increase within-group feeding competition, necessitating increased travel, an association presumed to constrain group size. Low group size, hence, is at times an indication of high competition induced by low food availability or inadequate habitat suitability (Clutton-Brock, 1975; Fimbel *et al.*, 2001; Teichroeb *et al.*, 2003). In Nyungwe, Rwanda, *Colobus angolensis ruwenzorii* form groups of up to 300 individuals (Fimbel, 2001; Fashing *et al.*, 2007a); they spend twice as much time feeding and six times as much traveling, at the cost of resting, compared to the coastal colobus of this study (see Table 2). Groups of *C. a. ruwenzorii* in Ituri Forest, D. R. Congo, with a mean group size of 14 (Bocian, 1997), show the same trend.

Travel and feeding activity also might be influenced by the availability of seasonal food sources. Different food items such as flowers, fruits or seed pods, often available in widely dispersed food trees, might require more travel or even feeding time than typically more abundant leaves.

Essential habitat for *Colobus angolensis palliatus* is being degraded and decreasing in extent. The subspecies' range currently includes only two large protected forests, Shimba Hills National Forest Reserve in Kenya and Mikumi National Park in Tanzania (Rodgers, 1981; Anderson *et al.*, 2005). Rapidly decreasing and remnant *Colobus angolensis palliatus* populations might drastically alter their behavior and exploit a wider range of food sources, including cultivated and non-indigenous plants (Moreno-Black & Maples, 1977; Chapman *et al.*, 2002; Anderson, 2005). This study provides preliminary data on the extent to which forest fragments have the potential to remain viable habitats and sheds light on colobine adaptions to coastal habitat. It is apparent that year-round and comparative studies focusing on *Colobus angolensis palliatus* feeding ecology, dietary flexibility and behavioral plasticity would increase knowledge of the subspecies and are essential to the development of more informed conservation and management plans.

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