

CHAPTER SIX

Geographic Variation in Savanna Baboon (*Papio*) Ecology and its Taxonomic and Evolutionary Implications

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ABSTRACT

Jolly (1993) stated that the degree of ecological niche separation among closely related taxa may help to distinguish their evolutionary relationships since ecological divergence is often thought of as a characteristic of true biological species. Based on qualitative data, Jolly (1993) hypothesized that there is little niche separation among savanna baboon forms and therefore suggested that they are a single species. In addition, a recent study by Frost and colleagues (2003) found that baboon cranial morphology covaried with latitude that also suggests a single species designation. This present study quantitatively examined the ecological niche space of savanna baboons to test Jolly's hypothesis and to examine how their ecological variation varied with geography. To investigate this idea, previously published long-term data were accumulated from over twenty savanna

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baboon populations. Variables from four categories were used to quantify their niche space: 1) Environment, 2) Diet, 3) Activity budget, and 4) Social organization. A discriminant function and principal components analysis was conducted for each dataset, and confirmed that savanna baboon subspecies inhabit significantly distinct environments, yet display a statistically non-significant difference in their diet, activity budget, and social organization. In addition, a hierarchical cluster analysis revealed that savanna baboon ecology followed a latitudinal cline. Therefore, the results of these analyses cannot falsify Jolly's hypothesis that there is little ecological niche separation among baboon taxa.

Key Words: ecogeography, biogeography, species concepts, speciation, niche, intraspecific

INTRODUCTION

Identifying and defining species has been a problem in biology for many years. Discussion of the species problem has made a resurgence recently due to the frequent disparity between the phylogeny and taxonomy of taxa (Hey, 2001; Sites and Marshall, 2003) and the importance of identifying species for conservation purposes (Isaac *et al.*, 2004). Baboon (*Papio*) taxonomy is one of the most contentious issues in primatology. Ecologically, savanna baboons are parapatrically distributed in a variety of habitat types, while consuming a broad array of dietary items, and demonstrating a wide range of behavioral activity patterns (Altmann, 1974; Jolly, 1993; Barton *et al.*, 1996; Henzi and Barrett, 2003). In addition to their ecological diversity, savanna baboons are quite varied in their body size, pelage color, craniodental anatomy, and other morphological traits (Hill, 1967; Jolly and Brett, 1973; Hayes *et al.*, 1990; Frost *et al.*, 2003).

The ecological and morphological geographic variation in savanna baboons is quite high compared to other primate taxa and is one reason that contributes to the uncertainty surrounding their taxonomy and evolutionary history. The two major taxonomic hypotheses, a single or multispecies classification, depend on the type of data and species concept utilized. The distinct morphological traits present in each baboon taxon lends support to a multiple species arrangement as defined by the phylogenetic species concept (Fleagle, 1999; Groves, 2001; Grubb *et al.*, 2003). This species concept relies on the idea that species display a unique combination of traits distinct from other such organisms within

the context of ancestry and descent (Cracraft, 1987; Kimbel and Rak, 1993). The phylogenetic species concept is commonly implemented by paleontologists since the available data of extinct animals are limited to anatomical structures.

Alternatively, the biological species concept defines a species as a group of individuals that interbreed or can potentially interbreed, and are reproductively isolated from other such groups (Mayr, 1942). The biological species concept is probably the most objective species concept since its definition relies on measuring gene flow among populations, yet it is often difficult to implement since genetic data are difficult to obtain in many circumstances. More recently, with the advent of molecular techniques, genetic data has been used to help solve this taxonomic puzzle. Molecular data from several baboon populations confirm the gene flow among baboon taxa, which would support the idea of a single baboon species if the biological species concept is employed (Rogers, 2000; Newman *et al.*, 2004). The seminal paper by Jolly (1993) combines these two species concepts by labeling baboons “phylogenetic subspecies”, acknowledging the phenotypic distinctiveness of each taxon, yet also accounting for the lack of reproductive isolation among them. I will adopt Jolly’s (1993) definition of savanna baboon forms as subspecies for the purposes of this investigation.

Traditionally, morphological traits have been used to examine animal taxonomy because these data were readily available from museum specimens and can be quantified relatively easily. In addition, a predominant school of thought is that morphological characters are less labile than behavioral or ecological traits, and therefore more useful in reconstructing a phylogeny or taxonomy (Atz, 1970; Wilson, 1975; Baroni Urbani, 1989). Alternatively, several more recent studies have shown that behavioral and ecological traits often exhibit similar levels of homoplasy as morphological traits (de Queiroz and Wimberger, 1993; Proctor, 1996; Wimberger and de Queiroz, 1996; Doran *et al.*, 2002). This is not surprising, because much of an animal’s behavior and ecology depends in part on morphological traits such as body mass, and feeding and locomotor adaptations (Fleagle, 1999; Alcock, 2001). Therefore, a species’ ecological niche is also influenced by its evolutionary history (Fleagle and Reed, 1999) and may be an interesting line of evidence in investigating taxonomic questions. In fact, Mayr (1982) altered his definition of the biological species concept to clarify that a species is, “. . . a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.”

The purpose of this chapter is to quantify the ecological variability in savanna baboons and place it in a geographic and taxonomic context. First, I examined the ecological variation within and between baboon subspecies in order to investigate whether baboons should be considered a single species. The logic for this analysis is based on Jolly's (1993) statement that the degree of ecological niche separation among taxa may help to distinguish their evolutionary relationships since ecological divergence is often thought of as a characteristic of true biological species. In addition, with respect to savanna baboons, Jolly stated that there is no niche separation or adaptive differences among the subspecies. This first analysis will quantitatively test Jolly's idea, where populations of a single species are expected to display similar niches, whereas populations from separate species should display distinctive ecological roles. Therefore, if the population's niche is defined by the environment in which they live, their diet, activity budget, and social organization, then there should be a significant difference among subspecies in these traits if they are truly separate species. Alternatively, a lack of significant differences in these traits should indicate a cohesive yet ecologically variable species. Second, the adaptive response of savanna baboon subspecies will be examined. If savanna baboons are a single species, then the effects of environmental factors on their diet, activity budget, and social organization should be similar. Alternatively, different species would be expected to display different responses to environmental characteristics. Lastly, the overall ecological similarity among savanna baboon subspecies was assessed in relation to their geographic distribution. This may also provide information regarding their taxonomic status. A recent paper by Frost *et al.* (2003) showed that the cranial morphometric variation of baboons follows a latitudinal cline which supports the genetic data of a single geographically varied species. An ecological distribution following a similar cline would corroborate this idea (Coyne and Orr, 2004; Fooden and Albrecht, 1993).

METHODS

Data Collection

Data were collected from published material from a total of 27 wild savanna baboon populations (Appendix 1). Data were gathered for 11 olive baboon populations, four yellow baboon populations, ten chacma baboon populations, and two guinea baboon populations. *Hamadryas* baboons were not included

since comprehensive long-term data are not available. The variables included in the analyses were chosen because of two criteria: (1) their biological relevance to a baboon's niche, and (2) their availability in the published literature. Based on these criteria, the analyses included the following variables that were grouped into four datasets: (1) *Environment*: (a) mean annual rainfall, (b) number of dry months, (c) altitude, (d) number of sympatric cercopithecoids, (e) predation risk (as defined by Hill and Lee, 1998), and (f) latitude. The broad-scale variables in the *Environment* dataset are important in shaping the abundance and distribution of vegetation in a habitat, as well as other factors that have significant effects on primate diet, activity budget, and social organization (Murphy and Lugo, 1986; Janson, 1992; Bronikowski and Altmann, 1996; Chapman *et al.*, 1999). (2) *Diet*: annual percentage of (a) fruit/seeds, (b) leaves, (c) flowers, (d) fauna, and (e) underground items. (3) *Activity budget*: percentage of time spent (a) resting, (b) social, (c) feeding, and (d) moving. (4) *Social organization*: (a) group size, (b) number of adult males, (c) number of adult females, and (d) adult sex ratio. The definition of social organization used in this study follows Kappeler and van Schaik (2002), as, “. . . the size, sexual composition and spatiotemporal cohesion of a society.” The spatiotemporal characteristics of the savanna baboon populations will not be included in the analyses since these data are rarely quantified by researchers, yet all populations are gregarious.

Social organization data were included in the analyses if the authors stated that group composition could be accurately determined. The diet and activity budget data used in this study were accumulated from sources with a research period of at least 10 months. Some populations were studied by more than one researcher and/or had data available for more than one social group, resulting in varied data produced for a single baboon taxon at a single study site (e.g., Amboseli). The mean value for these data was used in these cases.

Data Analyses

Two multivariate approaches were used to examine the amount of niche overlap among savanna baboon subspecies. Ideally, all datasets would be combined and entered into a single multivariate analysis, yet this would result in a reduced sample size since many populations do not have data for all variables. Consequently, to increase the sample size, each dataset was subjected separately to the multivariate analyses. It is important to note that another consequence of

having incomplete datasets is that each analysis was not comprised of identical populations to represent the variation in each subspecies.

First, a discriminant function analysis (DFA) was conducted to examine explicitly the within versus among subspecies ecological variation. Investigations comparing within versus among taxa morphological variation have been conducted many times using this analytical technique (see Albrecht, 1976; Shea and Coolidge, 1988 for examples; Hayes *et al.*, 1990; Froehlich *et al.*, 1991; Albrecht and Miller, 1993; Ford, 1994). There is no *a priori* reason to suggest that ecological data should perform any differently. DFA is used to test for differences among groups by maximizing the differences among them. In addition, it examines whether the independent variables suitably predict the *a priori* group assignments while controlling for covariation among predictor variables (Tabachnick and Fidell, 1989; McGarigal *et al.*, 2000). These group assignments are based on *a priori* knowledge of the partitioning of the samples, in this case, assigning a subspecies designation to each savanna baboon population. Guinea baboon populations were unclassified in the DFA since only one population had the available data for each dataset.

Two major assumptions of DFA are the multivariate normality of the data and that the variance-covariance matrices are homogenous among groups. The second assumption is the most critical and may lead to increased Type I or II error rates (depending on how sample size is related to variance) if not met (Tabachnick and Fidell, 1989; McGarigal *et al.*, 2000). All variables were tested for normality using Shapiro-Wilk normality tests. Those variables failing normality tests were log transformed. In addition, Levene's test of homogeneity of variance was conducted for each variable. Testing the univariate homogeneity of variance is usually a good indicator of the homogeneity of variance-covariance matrices (McGarigal *et al.*, 2000). The results of the DFA were examined more closely if it contained variables failing the Levene's test at the alpha level of 0.01. The results of the DFA were especially focused on the degree of subspecies overlap based on an examination of the discriminant function biplots (Gower and Hand, 1995). When DFA is used in this exploratory manner, the assumptions of the test can be relaxed (Tabachnick and Fidell, 1989). For each dataset, Pearson's correlations were conducted between the original variables and the discriminant functions to assess the importance of the original variables in distinguishing among the baboon groups.

Since discriminant function analyses have several statistical assumptions that may be difficult to check using a relatively small sample size, a principal

components analysis (PCA) was conducted as a complementary technique. A PCA is a strictly exploratory technique and as such, has fewer statistical assumptions (Tabachnick and Fidell, 1989). A correlation matrix was used as the basis of each PCA. The savanna baboon populations were plotted in multidimensional space to examine the degree of ecological overlap among subspecies. For each dataset, Pearson's correlations were conducted between the original variables and the principal component axes to assess the correlation between the original variables and the principal components.

A series of analysis of covariance (ANCOVA) tests were used to examine whether savanna baboon subspecies responded to environmental forces in the same manner. An ANCOVA was conducted with each variable in the *Diet*, *Activity Budget*, and *Social organization* datasets as the dependent variable. For all ANCOVAs the savanna baboon subspecies acted as the categorical predictor variable and the variables in the *Environment* dataset as the covariates. The alpha level for these analyses was corrected with a Bonferroni adjustment (Sokal and Rohlf, 1995).

Finally, a hierarchical cluster analysis was implemented to examine the overall ecological similarity among the savanna baboon subspecies in a geographic context. The population mean for each baboon subspecies was calculated for each variable. All data were standardized using z scores. The average Euclidian distances among taxa were calculated and taxa were joined using the unweighted pair group method with arithmetic mean (UPGMA) (Tabachnick and Fidell, 1989). The cluster analysis included all variables from the *Social organization*, *Diet*, and *Activity budget* datasets. The *Environment* dataset was not included in the cluster analysis because the dendrogram produced from the cluster analysis was mapped onto a distribution map of savanna baboons to examine the biogeographical pattern of savanna baboon ecology. Including the variables from the *Environment* dataset would be logically circular since many of the variables are geographic in nature.

All analyses were conducted with SPSS 11.0 and Statistica 6.0 for Windows. A p -value of <0.05 was considered significant for the DFAs and Pearson's correlations.

RESULTS

The discriminant function analysis of the *Environment* dataset yielded a significant difference among taxa, with all of the populations being correctly grouped

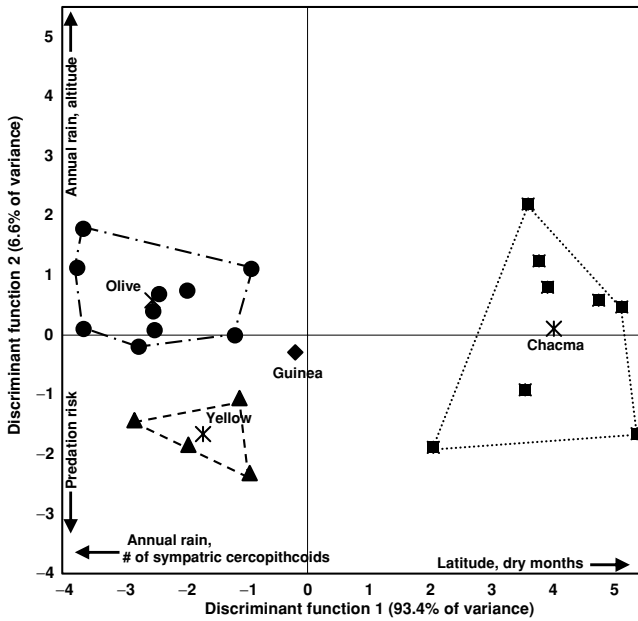
Table 1. Results of the discriminant function analyses

Dataset	Wilks' Lambda	Chi-square	<i>df</i>	<i>p</i> -value
Environment (with Latitude)	0.048	50.033	12	<0.001
Diet	0.212	13.941	10	0.176
Activity Budget	0.498	7.316	8	0.503
Social organization	0.383	11.993	8	0.152

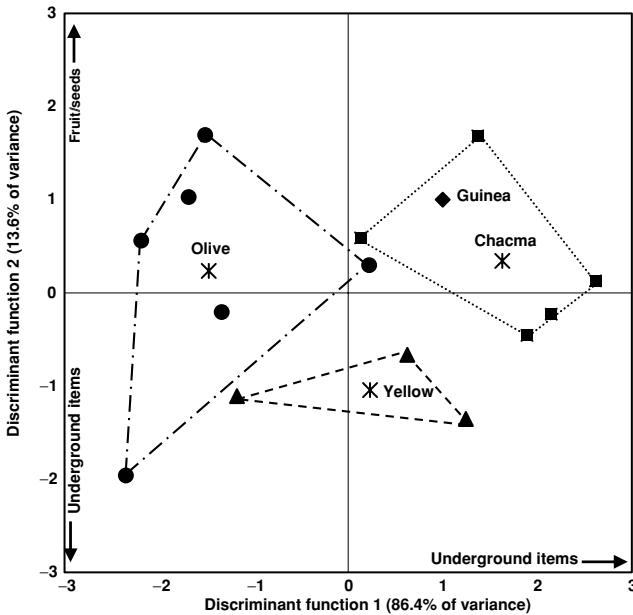
into their *a priori* classifications (Wilks' Lambda = 0.048, $p < 0.001$, $df = 12$) (Table 1). Latitude is the most important variable in this analysis, clearly separating the chacma baboons from the remaining groups on the first axis (Figure 1a). The number of sympatric cercopithecoids at a site and mean annual rainfall were additional variables that contributed to distinguishing chacma populations from the yellow and olive baboons. Function two of the analysis best discriminated olive from yellow baboons. The most important variables that correlated with function two were predation risk and annual rain (Table 2). The guinea baboon population is most similar to the olive and yellow baboon populations with respect to their environmental characteristics.

The *Diet*, *Activity budget*, and *Social organization* DFAs did not yield statistically significant results ($p = 0.176$, $p = 0.503$, $p = 0.152$, respectively) (Table 1), yet the majority of the populations were correctly classified (Table 3). Examining the DFA biplots from these datasets showed that the amount of overlap among subspecies for the *Diet* dataset was not high, yet was moderate for the *Activity budget*, and *Social organization* datasets (Figure 1b–d). In the *Diet* biplot, the chacma baboon populations were found in the right half of the biplot, which indicated a high proportion of underground items in their diet (Figure 1b). The olive baboons generally occupied the left half of the graph, indicating lower levels of underground food items. Yellow baboon populations were intermediate on this dietary axis. The second function of this DFA correlated most strongly with the consumption of fruit/seed and underground food items. Olive and chacma baboons overlapped greatly in the Y-axis, but yellow baboons showed higher levels of underground item intake and lower levels of frugivory. The diet of the guinea baboon population was most similar to that of the chacma baboons.

The *Activity budget* DFA produced a first function which accounted for nearly 90% of the variation in the dataset and is negatively correlated with time spent social (Figure 1c). The yellow baboon populations, along with one

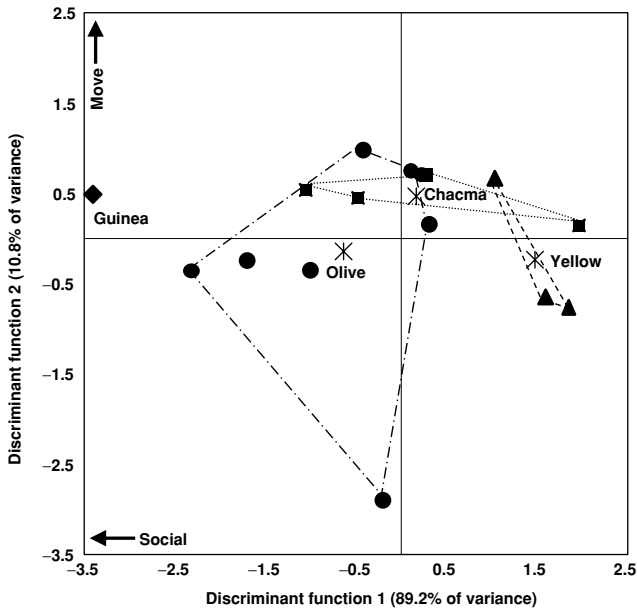


(a)

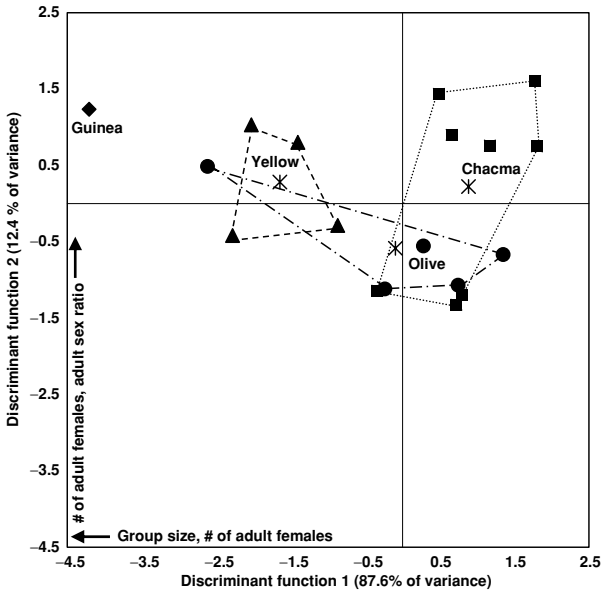


(b)

Figure 1. (a–d) Biplots of the discriminant function analysis for the (a) *Environment*, (b) *Diet*, (c) *Activity budget*, and (d) *Social organization* datasets. Symbols represent olive (●), yellow (▲), chacma (■), and guinea (◆) savanna baboon populations. The subspecies centroid (×) as calculated from the DFA is also displayed.



(c)



(d)

Figure 1. (Continued)

Table 2. Correlation coefficients between original variables and discriminant functions

Variable	Function 1	Function 2
Fruit/seed	0.012	0.554 ^a
Leaves	-0.483	0.246
Underground items	0.551 ^a	-0.562 ^a
Flowers	0.163	-0.090
Fauna	-0.258	-0.356
Feed	0.488	0.275
Move	-0.189	0.534 ^a
Rest	-0.172	-0.358
Social	-0.913 ^b	0.085
Group size	-0.804 ^b	0.425
# of males	-0.300	0.285
# of females	-0.797 ^b	0.670 ^b
Adult sex ratio	-0.136	0.558 ^a
Annual rain	-0.418 ^a	0.640 ^b
Dry months	0.509 ^a	-0.187
Altitude	-0.402	0.417 ^a
Latitude	0.982 ^b	0.122
Log (Sympatric cercopithecoids)	-0.705 ^b	0.096
Predation risk	-0.383	-0.770 ^b

^aCorrelation is significant at the 0.05 level (2-tailed).

^bCorrelation is significant at the 0.01 level (2-tailed).

chacma population (Drakensberg) devoted the least amount of time to social behavior. The olive baboons and the remaining chacma baboon populations displayed intermediate values for function one, with the lone guinea population (Assirik) located in the far left of the biplot indicating the highest level of time being social. The percentage of time spent moving significantly correlated with function two. The olive baboons varied considerably in relation to this axis,

Table 3. Percentage of correctly classified savanna baboon populations

Taxon	Environment	<i>N</i> ^a	Diet	<i>N</i>	Activity	<i>N</i>	Social Org	<i>N</i>	Taxon Mean	<i>N</i>
Olive	100.0	10/10	83.3	5/6	87.5	7/8	20.0	1/5	79.3	23/29
Yellow	100.0	4/4	66.7	2/3	66.7	2/3	75.0	3/4	78.6	11/14
Chacma	100.0	8/8	100.0	5/5	25.0	1/4	75.0	6/8	80.0	20/25
Dataset Mean	100.0	22/22	85.7	12/14	66.7	10/15	58.8	10/17	79.4	54/68

^aThe proportion of correctly classified populations

with yellow baboons displaying intermediate values. The chacma populations were less variable and displayed relatively high values. The single guinea baboon population at Assirik displayed an intermediate level of time allocated to moving.

The biplot from the *Social organization* DFA exhibited the most overlap among savanna baboon subspecies, especially between olive and chacma populations (Figure 1d). Mean group size and the number of adult females in a group negatively correlated with function one. Yellow baboons tended to have the highest values, followed by olive populations, with chacma baboons having the lowest scores. The guinea baboon population from Badi exhibited the highest function one score of all the savanna baboon populations.

Two variables from the *Environment* dataset, predation risk and the number of sympatric cercopithecoids, failed the Shapiro-Wilk normality test. Both variables were subsequently log transformed, yet transforming predation risk still yielded non-normal results. Consequently, the untransformed data were used in the analyses. The results of the Levene's tests showed that one variable (predation risk) exhibited significantly different variances among subspecies at the $p < 0.01$ level (Table 4). The violation of this DFA assumption most likely

Table 4. Results from Levene's test of homogeneity of variance

Variable	Levene's statistic	<i>df</i> 1	<i>df</i> 2	<i>p</i> -value
Annual rain	1.451	2	19	0.259
Dry months	0.050	2	19	0.951
Altitude	3.936	2	19	0.037
Latitude	0.738	2	19	0.491
Log (Sympatric cercopithecoids)	1.211	2	19	0.320
Predation risk	8.023	2	19	0.003
Fruit/seed	0.334	2	12	0.722
Leaves	6.476	2	12	0.012
Underground items	2.507	2	12	0.123
Flowers	1.272	2	12	0.315
Fauna	4.403	2	12	0.037
Feed	1.704	2	12	0.223
Move	1.542	2	12	0.253
Rest	4.708	2	12	0.031
Social	1.778	2	12	0.211
Group size	0.085	2	14	0.919
# of males	2.282	2	14	0.139
# of females	0.598	2	14	0.563
Adult sex ratio	1.321	2	14	0.298

did not have a substantial effect since predation risk was the least important variable separating the taxa on the first axis.

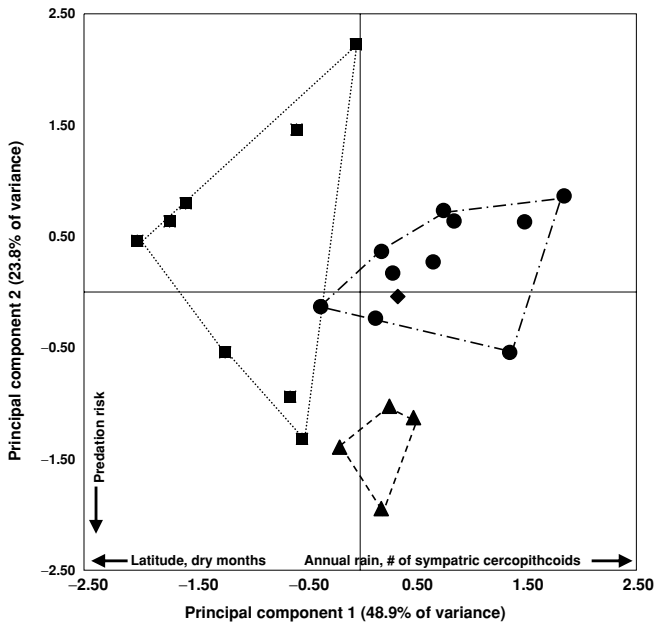
Although a PCA does not statistically test for differences among groups, the PCA biplots showed that there is a lack of differentiation among savanna baboon subspecies (Figure 2a–d). The PCA biplot of the *Environment* dataset (Figure 2a) displayed the least overlap among subspecies, similar to the DFA results. The PCA results of the remaining datasets (Figure b–d) displayed more overlap among subspecies compared to the DFA results. The eigenvalues for all principal components analyses are presented in Table 5, with the correlation coefficients between the original variables and the principal components listed in Table 6. The PCA analyses support the non-significant differences among savanna baboon subspecies for these traits. Overall, maximizing the differences among subspecies using the DFA analyses did not yield statistically significant results, and this was supported by the PCA biplots.

The ANCOVAs resulted in no significant difference among the *Diet*, *Activity budget*, and *Social organization* variables among subspecies (Table 7). These tests suggest that the baboon subspecies respond to environmental factors in a similar fashion and therefore show similar adaptive responses.

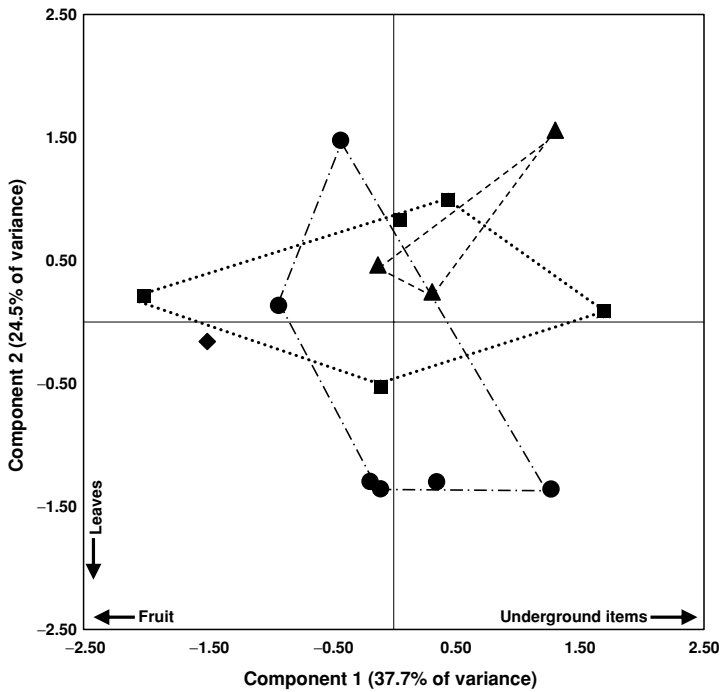
The results of the UPGMA cluster analysis demonstrated that chacma and yellow baboons were the most ecologically similar, followed by olive baboons, with guinea baboons being the most distinct taxon. When these results were plotted on a map displaying the geographic distribution of savanna baboons, ecological similarity followed a latitudinal cline (Figure 3).

DISCUSSION

The result of this study lends support to Jolly's (1993) conclusion, that savanna baboon subspecies are ecologically similar. There was a statistically significant difference among the savanna baboon subspecies in only one of the datasets (*Environment*). The results of the remaining DFA analyses showed that each subspecies displayed trends in certain niche characteristics, yet these differences were not sufficient to yield statistically significant results. In addition, the PCA analyses corresponded to the DFA tests showing lack of separation among the subspecies in the *Diet*, *Activity budget*, and *Social organization* datasets. These results show that the ecological variability among savanna baboon subspecies does not exceed the variation within subspecies. Finally, the ANCOVAs



(a)



(b)

Figure 2. (a–d) Biplots of the principal components analysis of the (a) *Environment*, (b) *Diet*, (c) *Activity budget*, and (d) *Social organization* datasets. Symbols represent olive (●), yellow (▲), chacma (■), and guinea (◆) savanna baboon populations.

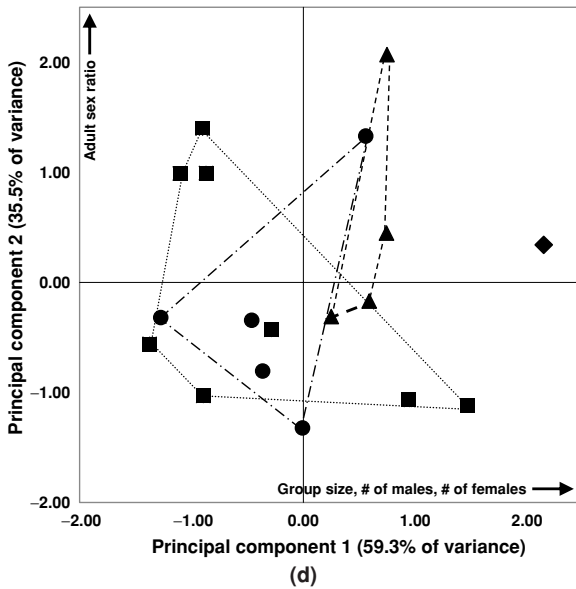
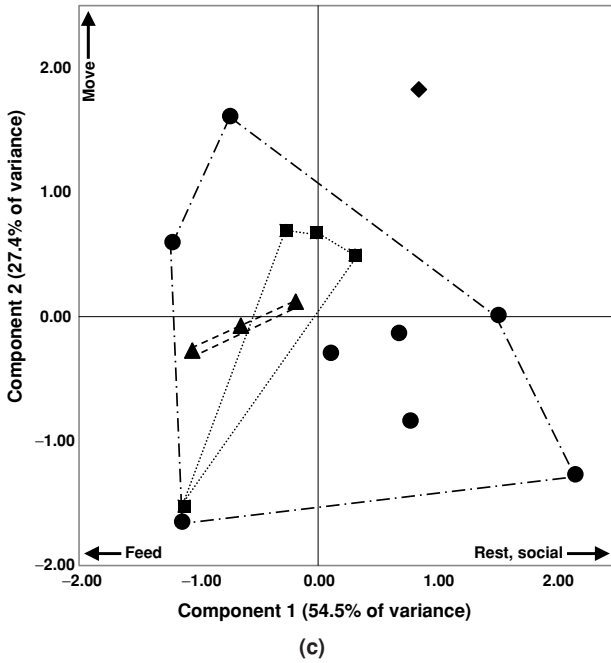


Figure 2. (Continued)

Table 5. Eigenvalues for the principal components analyses

Dataset	Comp1	Comp2	Comp3	Comp4	Comp5	Comp6
Environment (with Latitude)	2.977	1.274	0.929	0.399	0.253	0.168
Diet	1.885	1.225	1.046	0.805	0.039	–
Activity Budget	2.182	1.096	0.689	0.033	–	–
Social organization	2.373	1.421	0.154	0.051	–	–

suggest that the dietary, activity budget, and social organization characteristics of savanna baboon subspecies are shaped by environmental factors in a similar way.

A closer examination of the DFA results demonstrated that the Social Organization dataset had the least success at correctly predicting the subspecies of populations compared to the other datasets. This lower degree of variability in these variables may support Dunbar's proposal (1992) that baboons maintain their group size in varying environments by adjusting their activity budget.

Table 6. Correlation coefficients between the original variables and the principal components

Variable	Comp1	Comp2	Comp3	Comp4	Comp5	Comp6
Fruit/seed	–0.985 ^b	0.089	–0.053	0.023	0.136	–
Leaves	0.492	–0.739 ^b	–0.151	0.426	0.083	–
Underground items	0.779 ^b	0.433	–0.215	–0.385	0.108	–
Flowers	0.101	–0.313	0.890 ^b	–0.313	0.037	–
Fauna	0.235	0.621 ^a	0.426	0.614 ^a	0.023	–
Feed	–0.937 ^b	–0.286	0.155	0.127	–	–
Move	–0.075	0.993 ^b	0.079	0.054	–	–
Rest	0.911 ^b	–0.127	–0.374	0.115	–	–
Social	0.684 ^b	–0.113	0.720 ^b	0.026	–	–
Group size	0.911 ^b	0.286	–0.292	0.045	–	–
# of males	0.814 ^b	–0.540 ^a	0.169	0.130	–	–
# of females	0.933 ^b	0.290	0.151	–0.148	–	–
Adult sex ratio	–0.094	0.981 ^b	0.133	0.102	–	–
Annual rain	0.722 ^b	0.459 ^a	–0.388	0.031	0.310	–0.139
Dry months	–0.821 ^b	–0.172	0.326	–0.285	0.330	–0.019
Altitude	0.444 ^a	0.425 ^a	0.745 ^b	0.239	0.074	0.071
Latitude	–0.806 ^b	0.320	–0.337	0.241	0.107	0.256
Log (Sympatric cercopithecoids)	0.898 ^b	–0.108	–0.051	–0.315	0.044	0.278
Predation risk	0.357	–0.860 ^b	–0.024	0.321	0.170	0.025

^aCorrelation is significant at the 0.05 level (2-tailed).

^bCorrelation is significant at the 0.01 level (2-tailed).

Table 7. ANCOVAs examining the relationship between *Environment* and *Diet*, *Activity budget*, and *Social organization* among savanna baboon subspecies

Variable	<i>F</i> (<i>df</i>)	<i>p</i> -value
Fruit/seed	0.874 (2, 4)	0.484
Leaves	1.045 (2, 4)	0.432
Underground items	1.776 (2, 4)	0.281
Flowers	0.311 (2, 4)	0.749
Fauna	0.779 (2, 4)	0.518
Feed	3.269 (2, 6)	0.109
Move	0.969 (2, 6)	0.432
Rest	2.352 (2, 6)	0.176
Social	1.187 (2, 6)	0.367
Group size	0.751 (2, 6)	0.512
# of males	2.506 (2, 6)	0.162
# of females	2.367 (2, 6)	0.175
Adult sex ratio	0.334 (2, 6)	0.729

Bonferroni corrected *p*-values are significant at the 0.01 level for the *Diet* dataset and 0.0125 for the *Activity budget* and *Social organization* datasets.

Although the results of this study showed that savanna baboon subspecies inhabit significantly different environments, their diet, activity budget, and social organization do not exhibit a corresponding distinctiveness. These results do not necessarily contradict the well established idea that environmental factors are an important influence in shaping primate behavior and ecology (Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977; van Schaik and van Hooff, 1983; Janson, 1992). The genetic cohesiveness of savanna baboon subspecies may be the cause of this disparity. Baboons are generally regarded as ecologically flexible (Post, 1981; Barton *et al.*, 1992; Barton and Whiten, 1993), yet there may be a limit to this flexibility due to gene flow. It has been shown that even low levels of genetic introgression among populations are enough to produce homogenizing effects (Ridley, 1997; Futuyma, 1998; Coyne and Orr, 2004).

Geographic Variation and Species Concepts

The idea that species exhibit a unique set of traits separate from other species is central to the phylogenetic species concept (Cracraft, 1987). The distinguishing morphological features displayed by each baboon subspecies include pelage, body size, and dental attributes (Hill, 1967; Jolly and Brett, 1973; Hayes *et al.*,

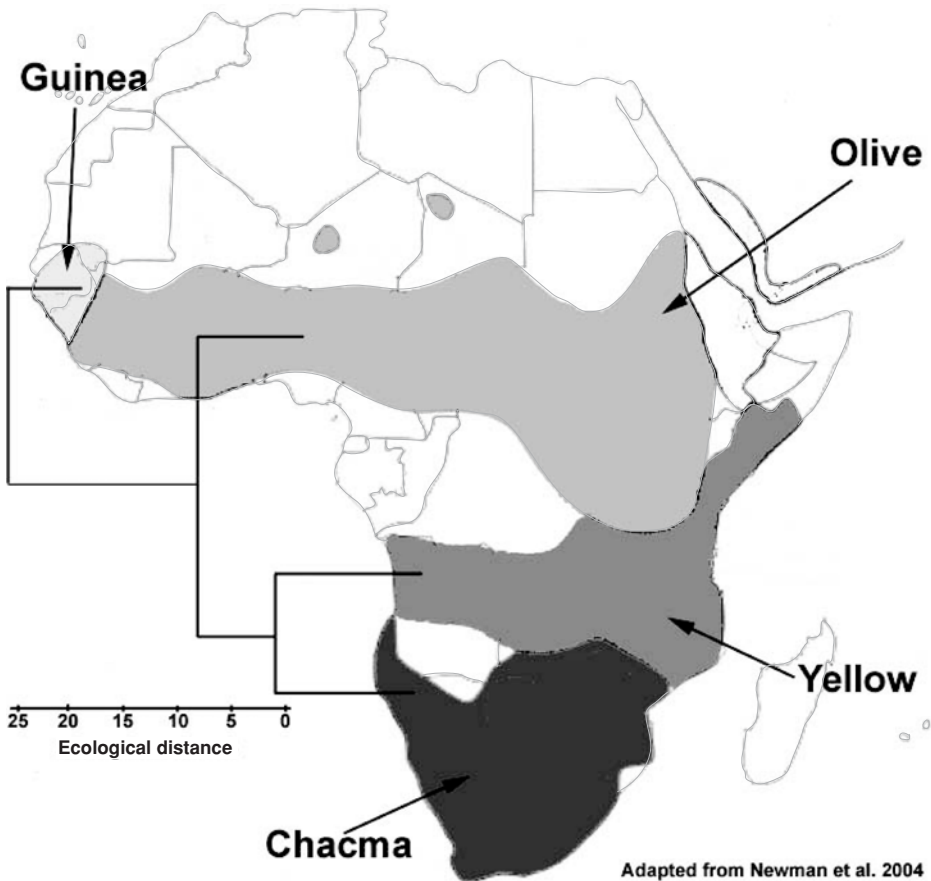


Figure 3. Geographic range of savanna baboon subspecies and their overall ecological niche similarity based on a UPGMA cluster analysis using a multivariate Euclidian distance matrix. Map adapted from Newman *et al.*, 2004.

1990). Yet, as Jolly (1993) aptly pointed out, suggesting that these taxa are full species would be ignoring the knowledge that there is gene flow among them. The hybridization of olive and hamadryas, and olive and yellow baboons has been well documented (Nagel, 1971; Nagel, 1973; Samuels and Altmann, 1986). The genetic cohesiveness of these taxa is evidenced by the production of non-sterile hybrids, yet the relative fitness of these hybrids is not known (Phillips-Conroy *et al.*, 1991; Woolley-Barker, 1999; Beehner and Bergman, 2003). On the basis of this genetic information, a single baboon species should be adopted by proponents of the biological species concept (Mayr, 1942).

Jolly (1993) solves the discordance between the two taxonomic arrangements by stating that baboons are a single polytypic species (“phylogenetic subspecies”). This idea acknowledges the distinctiveness of each taxon while accounting for the gene migration among them. The results of this study support Jolly’s hypothesis. In addition, the allopatric nature of baboons suggests a recent divergence among populations. The amount of overlap among populations should increase with divergence time as populations achieve full species status and shift their geographic range (Losos and Glor, 2003). Therefore, if savanna baboon subspecies were indeed full species, we should expect more range overlap among them.

The idea that savanna baboons are a single species is also supported by ecological and biogeographical data within the ecological species concept. This species concept defines a species as a collection of allopatric populations occupying a more similar niche to each other than any other population in their geographic range (van Valen, 1976). The savanna baboon taxa displayed a relatively low degree of ecological niche separation. Other sympatric species that approximate the savanna baboon niche are the vervet monkey (*Chlorocebus aethiops*) and patas monkey (*Erythrocebus patas*) (Fleagle, 1999). A future study concurrently examining the quantitative niche space of savanna baboon, vervet monkey, and patas monkey populations may support this idea.

An interesting contrast to the idea that savanna baboons are a cohesive ecological species may be found with guenon monkeys (*Cercopithecus* spp.). Guenon species occupy a similar ecological niche to each other compared to other sympatric primate taxa, with lineages diverging relatively recently (Ruvolo, 1988; Struhsaker *et al.*, 1988; Disotell and Raaum, 2002). Yet, compared to baboons, an important distinction in guenons is that they are often found in sympatric associations with other *Cercopithecus* species while maintaining high degrees of reproductive isolation (but see Struhsaker *et al.*, 1988 for cases of hybridization; Detwiler, 2002), and thus maintain species’ identities. This biogeographic contrast to baboons, and the resulting differences in the degree of reproductive isolation among closely related taxa, may be a vital clue to the idea that baboons are a single, ecological generalist species that occupy a broad niche, whereas guenons comprise many species that are ecological specialist, each occupying a narrow niche space (Kamilar, 2004).

Does Savanna Baboon Ecology Reflect their Evolutionary History?

A recent study examining the genetic relatedness of baboon populations has found that chacma baboons are the most basal lineage, followed by guinea, and hamadryas baboons, with the olive/yellow baboon clade diverging most recently (Newman *et al.*, 2004). The purpose of the study was not to investigate the possible taxonomic arrangement of baboons; rather it focused on the molecular relationships among baboon taxa. The branching pattern of this phylogenetic analysis does not correlate with the current geographical distribution of savanna baboon subspecies. The fact that the phylogeny of baboon taxa does not correlate with their geography suggests that the dispersal of individuals is not limited by geographic barriers (Epperson, 2004). In addition, the typology of the molecular phylogeny is not congruent with the phenogram representing the overall ecological similarity among these subspecies, which follows a latitudinal cline. The disparity between the evolutionary and ecological relationships may represent the effects of environmental traits in shaping the ecology of savanna baboons.

When comparing within versus among subspecies variation it is interesting that the lack of clear ecological differentiation among subspecies is in contrast to their morphological differences. Previous research examining morphological variation among baboon subspecies has noted that there is little overlap in the variation in odontometric traits (Hayes *et al.*, 1990) and pelage color (Hill, 1967). This discordance between morphological and ecological labiality may be unexpected to some. Traditionally, morphological data are often thought to be more highly conserved among closely related taxa, with behavioral and ecological traits more easily affected by environmental characteristics (Wilson, 1975). The ecological uniformity among subspecies may lend support to some more recent studies suggesting that behavioral and ecological traits do not display more homoplasy than morphological characters (de Queiroz and Wimberger, 1993; Proctor, 1996; Doran *et al.*, 2002).

Clinal Variation in Savanna Baboon Biology

The dendrogram produced by the cluster analysis and its projection on a map of Africa suggests that the ecological variation found in savanna baboons corresponds to a latitudinal cline. Biological clines have been observed in many non-primate taxa. Perhaps the best known is Bergmann's rule, where

species in colder climates tend to exhibit larger body sizes. This has been illustrated in several mammalian taxa including kangaroos (*Macropus giganteus*) (Yomtov and Nix, 1986), kangaroo rats (*Dipodomys* spp.) (Baumgardner and Kennedy, 1993), and small carnivores (*Lupus* spp. and *Vulpes* spp.) (Rosenzweig, 1968).

In primates, investigations of the relationship between latitudinal and phenotypic variation are relatively rare. Yet, the existing studies that examined this relationship have produced interesting results. Fooden and Albrecht (1993) found that *Macaca fascicularis* skull size covaried with latitude throughout their range in southeast Asia. Additionally, an earlier study by Albrecht (1976) is especially relevant to this current study. Albrecht examined cranial variation in several macaque taxa distributed throughout Sulawesi to examine their taxonomy and evolution. Albrecht found that these macaques displayed discrete morphological breaks and did not display variation correlated with their latitudinal distribution. These results led the author to conclude that these taxa should indeed be recognized as full species. In a contrasting scenario to Albrecht's study, is the recent paper by Frost and colleagues (2003). These researchers showed that baboon cranial shape and size displayed variation along a north-south geographic cline. They argue that these results support a single species hypothesis, since multiple species should display some degree of character displacement in adjacent taxa and not a clinal pattern in morphology. The results of this current study support the findings of Frost and colleagues.

The concordance between the relationships of eco-behavioral and cranial morphometric similarity with latitude suggests that variation in savanna baboon biology may be tied to broad-scale climatic factors that correlate with latitude. In addition, the clinal relationship between latitude and ecology and cranial morphology may suggest that baboons are currently in an intermediate stage of parapatric speciation. The "clinal model" of parapatric speciation proposes that a single species has a continuous distribution through a variable environment and that the populations are locally adapted to their environmental conditions (Fisher, 1930). Eventually, enough local adaptations will evolve to produce reproductively isolated taxa that become full species (Endler, 1977). Unfortunately, we can not be sure if the ecological and morphological variation exhibited by baboons are adaptations to local environmental factors or the result of developmental plasticity with no substantial change in allele frequencies among populations (Foster and Endler, 1999). Perhaps further studies can address this question.

CONCLUSIONS

The results of this chapter showed that there is no clear differentiation among the ecologies of savanna baboon subspecies. Therefore, these results cannot reject Jolly's (1993) hypothesis that non-hamadryas baboon taxa lack ecological separation. In addition, the ecological variation that does exist corresponds to a latitudinal cline. This supports Jolly's (1993) concept that savanna baboons are currently in some intermediate stage of the speciation process where they can be best described as "phylogenetic subspecies". The ecological data support the hypothesis that savanna baboons are a single species. Although it is useful to have animals classified as species or subspecies, our current ideas about species concepts may not be sufficient to apply them to all organisms, with baboons possibly being a good example of this (Hey, 2001). Recent and future studies of baboon biology at the subspecific level may shed more light on the nature of extant baboon taxonomy and evolutionary history (e.g., Frost *et al.*, 2003; Kamilar, 2004; Newman *et al.*, 2004).

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APPENDIX I. Ecological data from savanna baboon populations

Site	Taxon	Mean group size	Mean # of males	Mean # of females	Mean adult sex ratio	Mean annual rainfall
Chololo	olive	43.30	5.30	10.70	2.02	476
Gilgil	olive	66.40	5.10	21.42	3.83	691
Gombe	olive	35.33	7.13	11.88	1.65	1450
Q. E. Nat Park	olive	45.00	9.50	10.50	1.11	746
Shai Hills	olive	23.70	3.20	7.10	2.22	1065
Budongo	olive	43.00	-	-	-	1495
Mulu	olive	22.00	-	-	-	1105
Awash	olive	55.00	-	-	-	550
Bole	olive	20.00	-	-	-	1100
Kibale	olive	-	-	-	-	1662
Masai Mara	olive	-	-	-	-	-
Amboseli	yellow	48.00	9.00	21.00	2.35	423
Tana	yellow	78.80	4.60	21.80	4.74	494
Mikumi	yellow	51.70	7.70	16.00	2.08	851
Ruaha	yellow	72.00	7.00	19.00	2.71	304
Cape Good Hope	chacma	31.80	2.80	12.80	4.57	631
De Hoop	chacma	30.50	2.50	10.00	4.00	428
Honnet/Transvaal	chacma	47.20	13.00	20.50	1.58	307
Namib(Kuiseb)	chacma	28.00	5.70	7.70	1.35	18
Moremi	chacma	69.50	14.30	19.70	1.38	457
Cape Point	chacma	85.00	-	-	-	631
Suikerbosrand	chacma	78.00	-	-	-	700
T. Leopard Park	chacma	34.30	3.00	11.80	3.93	85
Mkuzi	chacma	47.30	6.00	11.30	1.88	630
Drakensberg	chacma	19.20	3.40	6.60	1.94	1149
Badi	guinea	83.00	12.00	31.00	2.58	-
Assirik	guinea	184.00	-	-	-	954

(Continued)

APPENDIX I. (*Continued*)

Site	# of dry months (<50 mm)	Altitude (meters)	Latitude	# of sympatric cercopithecoids	Predation risk
Chololo	8	1661	0	2	2
Gilgil	6	1765	0	1	2
Gombe	4	680	4	5	3
Q. E. Nat Park	4	990	0	6	1
Shai Hills	4	1000	5	2	2
Budongo	2	1050	1	4	2
Multu	6	1050	9	1	2
Awash	9	1400	8	1	2
Bole	6	2000	9	3	2
Kibale	3	1500	0	7	2
Masai Mara	-	-	-	-	-
Amboseli	9	1140	1	1	3
Tana	8	55	1	4	3
Mikumi	6	550	7	3	3
Ruaha	3	1230	7	1	3
Cape Good Hope	10	10	31	0	1
De Hoop	11	10	34	0	1
Honnnet/Transvaal	-	-	-	-	2
Namib(Kuiseb)	-	-	24	-	1
Moremi	7	300	19	1	3
Cape Point	8	10	34	0	1
Suikerbosrand	7	1600	27	1	1
T. Leopard Park	11	1060	22	1	2
Mkuzi	6	125	27	1	3
Drakensberg	5	2045	29	1	1
Badi	-	-	-	-	2
Assink	3	150	13	2	2

Chotolo	.40	.36	.15	.08
Gilgil	.51	.30	.08	.09
Gombe	.26	.19	.30	.11
Q. E. Nat Park	—	—	—	—
Shai Hills	.20	.18	.39	.23
Budongo	.59	.18	.06	.17
Mulu	.41	.25	.22	.15
Awash	.31	.25	.31	.12
Bole	.21	.25	.35	.16
Kibale	—	—	—	—
Masai Mara	—	—	—	—
Amboseli	.46	.26	.19	.09
Tana	—	—	—	—
Mikumi	.37	.26	.25	.06
Ruaha	.47	.24	.17	.05
Cape Good Hope	—	—	—	—
De Hoop	.40	.31	.16	.13
Honnnet/Transvaal	—	—	—	—
Namib(Kuiseb)	—	—	—	—
Moremi	—	—	—	—
Cape Point	.34	.29	.26	.11
Suikerbosrand	—	—	—	—
T. Leopard Park	—	—	—	—
Mkuzi	.36	.30	.21	.12
Drakensberg	.57	.18	.17	.08
Badi	—	—	—	—
Assirik	.24	.37	.21	.19

(Continued)

APPENDIX I. (Continued)

Site	% fruit/seed in diet	% leaves in diet	% underground items in diet	% flowers in diet	% fauna in diet	References
Chololo	.23	.27	.15	.21	.01	1, 2, 3, 4, 5, 6
Gilgil	.10	.53	.27	.03	.02	1, 2, 5, 6
Gombe	.49	.14	.07	.02	.13	1, 2, 7, 8
Q. E. Nat Park	—	—	—	—	—	9, 10
Shai Hills	.59	.08	.17	.05	.00	1, 2, 12, 18
Budongo	—	—	—	—	—	1, 13, 19
Mulu	—	—	—	—	—	1
Awash	—	—	—	—	—	1
Bole	.41	.41	.01	.12	.04	1, 11, 14, 17
Kibale	.72	.08	.00	.00	.20	14
Masai Mara	.46	.44	.08	.01	.01	15
Amboseli	.23	.15	.33	.04	.01	1, 14, 16, 17, 18, 19, 20
Tana	.53	—	—	.06	—	2, 14, 21
Mikumi	.43	.14	.12	.20	.10	1, 2, 22, 23
Ruaha	.16	.19	.52	.01	.09	1, 2, 23
Cape Good Hope	—	—	—	—	—	14
De Hoop	.35	.13	.42	.05	.05	24
Honnert/Transvaal	—	—	—	—	—	14, 25
Namib(Kuiseb)	—	—	—	—	—	14, 26
Moremi	—	—	—	—	—	2, 26, 27, 28
Cape Point	.42	.25	.16	.12	.03	1, 29
Suikerbosrand	.43	.08	.39	.07	.03	30
T. Leopard Park	—	—	—	—	—	14, 31
Mkuzi	.90	.06	.01	.03	.01	2, 32, 33
Drakensberg	.03	.26	.53	.14	.04	1, 2, 34
Badi	—	—	—	—	—	14
Assirik	.74	.09	.03	.09	.01	1, 35

- (1) Lee, 1999, (2) Hill *et al.*, 2000, (3) Kenyatta, 1995, (4) Barton, 1989, (5) Harding, 1976, (6) Eley *et al.*, 1989, (7) Oliver and Lee, 1978, (8) Ransom, 1981, (9) Hill and Lee, 1998, (10) Spinage, 1970, (11) Dunbar and Dunbar, 1974, (12) Depew, 1983, (13) Patterson, 1976, (14) Fleagle *et al.*, 1999, (15) Popp, 1978, (16) Post *et al.*, 1980, (17) Muruthi, 1997, (18) Bronikowski and Altmann, 1996, (19) Alberts *et al.*, 1996, (20) Post, 1981, (21) Bentley-Condit and Smith, 1997, (22) Norton *et al.*, 1987, (23) Rasmussen, 1978, (24) Hill, 1999, (25) Stoltz and Saayman, 1970, (26) Hamilton *et al.*, 1976 (27) Hamilton *et al.*, 1975, (28) Cheney *et al.*, 2004, (29) Davidge, 1978, (30) Anderson, 1981, (31) Cowlishaw, 1999 (32) Ron *et al.*, 1996, (33) Gaynor, 1994, (34) Whiten *et al.*, 1987, (35) Sharman and Dunbar, 1982

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