Evolutionary Ecology Research, 2008, **10**: 517–536

Time management in great apes: implications for gorilla biogeography

Julia Lehmann,[1,2]* Amanda H. Korstjens[1,3] and R.I.M. Dunbar[1,4]

[1] *British Academy Centenary Research Project, School of Biological Sciences, University of Liverpool, Liverpool,* [2]*School of Human and Life Sciences, Roehampton University, London,*
[3]*School of Conservation Sciences, Bournemouth University, Poole and*
[4]*Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford, UK*

ABSTRACT

Question: Do individual time budgets constrain a species' biogeographical distribution and group size?

Data studied: We used published data on gorilla behaviour and ecology as well as published climate variables to model their spatial distribution across Africa.

Method: We develop a mathematical model, based on the assumption that time is a fundamental ecological constraint. This novel approach uses the relationships between climatic variables and gorilla ecology and behaviour to calculate maximum ecological tolerable group sizes (and, from these, biogeographical distribution) for gorillas throughout Africa.

Results: We show that the most critical variable limiting the distribution of gorillas is resting time, which in turn is related to the composition of their diet. Thus, the model demonstrates that time constraints on individual behaviour can explain species' biogegraphical distributions as well as group sizes.

Keywords: activity budget, biogeography, gorilla, group size, time budget model.

INTRODUCTION

Although there has been a tendency for ecological research to focus on the relationship between climatic or ecological variables and species distributions (Mysterud *et al.*, 2000; Hill and Dunbar, 2002; Post and Forchhammer, 2002; Sergio, 2003) and these have proved to be of particular value for conservation biology (Kay *et al.*, 1997; Erasmus *et al.*, 2002), it is behaviour that ultimately interfaces between the environment and a species' ability to survive at a particular location. In general, an animal's capacity to survive in a particular habitat must depend on its ability to meet both its energetic demands and its time allocation demands. Although activity budgets have been of interest for a long time in many species (Klein and Fairall, 1986; Wirtz and

---

* Address all correspondence to Julia Lehmann, School of Human and Life Sciences, Roehampton University, Whitelands College, Holybourne Avenue, London SW15 4JD, UK. e-mail: j.lehmann@roehampton.ac.uk

Oldekop, 1991; Adamczak, 1999; du Toit and Yetman, 2005; Turner *et al.*, 2005), they have not been used to make inferences about a species' ability to survive in a habitat. By incorporating time and/or energy into models of the environment–biogeography relationship, we can gain considerable insight to why a species' distribution is constrained and what evolutionary pressures may have shaped this. This may be especially important for highly social species for whom the mere capacity to balance daily nutrient flow may not on its own be sufficient to ensure the species' presence at a particular location. Highly social species will only be able to live in a given habitat if that habitat can support group sizes that exceed some minimum value. Otherwise, an Allee effect (Stephens and Sutherland, 1999) will kick in, leading to the species' rapid local extinction, which may be accelerated in highly social species where minimum group sizes may be determined by local vulnerability to predation risk (Dunbar, 1988, 1996).

Nutrients (and especially energy) have traditionally been viewed as the limiting resource in population ecology (Rickleffs, 1970); in contrast, it has invariably been assumed that most animals have ample time in which to meet their biological needs, a claim implicitly justified on the grounds that animals spend a significant proportion of their day resting when they could seemingly be doing other biologically more useful things [the 'laziness' hypothesis (Herbers, 1981)]. However, resting time is not always convertible into other activities (Dunbar, 1992b, 1996) and time itself can be a critical resource, especially in species whose circadian rhythms prevent them from being active throughout the 24-h day. Optimal foraging theory (MacArthur and Pianka, 1966) acknowledges the importance of time efficiency when foraging but it is rarely applied to include all essential activities an animal carries out each day. In contrast, Dunbar (1996) used time budget models that explicitly focus on the complete time allocation demands that animals face in specific habitats.

Time budget models are built around the assumption that climatic and environmental variables influence vegetation quality and distribution (related to, for example, food and shelter), and thereby dictate how much time an animal has to spend feeding and moving to meet its daily nutritional intake requirement. These models further assume that resting time is made up of two components: enforced resting time, which is mostly dictated by thermoregulatory requirements (Stelzner, 1988) and/or the costs of food processing [e.g. digestion or, in ungulates, rumination (van Soest, 1982)], and the remainder, which is essentially free time, available either for genuine inactivity or for activities that are more directly related to other social or reproductive functions (Dunbar, 1992b, 1996). In addition, intensely social species living in bonded groups (like most primates) also require time for social interactions, which provide an essential 'glue' that maintains the temporal and spatial cohesion of social groups. This is reflected in a close relationship between social group size and social time in these species (Dunbar, 1991; Lehmann *et al.*, 2007b). Since time is limited, we can determine the maximum group size that any such species can support in a given habitat by determining (a) how competitive regimes affect time budget components and (b) how much time is available for social interaction once the demands for feeding, moving, and resting time have been set by the local environmental parameters (Dunbar, 1996). This, in turn, allows us to determine where the species can live, since, to occupy a particular location, the animals must be able to balance their activity budgets well enough to maintain groups of a minimum size. It is important to note that these models are necessarily taxon-specific because they rely on the way a taxon's specific physiological adaptations interact with climatic and vegetation variables.

In this study, we use a time budget model to investigate the variables that affect gorilla (*Gorilla* sp.) biogeography. Gorillas are a highly endangered species and an understanding of the effects of climatic conditions on their socioecology and biogeography is critical for their future survival. In addition, gorillas have proved particularly difficult to study (mainly due to their preference for heavily forested habitats), and the scarcity of good quality data on which to build a model provides an especially challenging case study with which to test the viability of our approach.

The aims of our study are twofold. First, we establish equations for each of the gorilla time budget components, thereby also providing information about the potential costs of group-living in gorillas. Second, we use these equations to model gorilla maximum ecologically tolerable group sizes, and use these to explore the species' biogeography.

METHODS

The data

We reviewed 192 publications on gorilla behaviour for studies providing quantitative data on gorilla group sizes and structure, time budgets, diet, and ranging patterns. In total, data from 18 different locations were collated. Tables 1 and 2 summarize climatic and behavioural data from 10 study sites for which data on time budgets were found, while Table 3 lists the references from which those data were taken as well as additional sites for which only information on diet or density was available. Both eastern and western gorillas were included in the analyses. If data from several years/studies were available for one population, we primarily used demographic data from those years for which we had time budget data. However, if either no time budget data were found or time budgets were available for several years, we averaged the data over the available years to yield one datum per study site so as to ensure statistical independence. In some cases, time budgets were available for combined categories (resting + moving or feeding + moving). In these cases, we first estimated moving time for that site using the equation in Table 4 and subtracted this from the respective time budget component to give a value for the other activity. Data on feeding time derived from Bai habitats (forest clearings in the Congo basin) were not used in our equation-finding process, because gorillas usually enter these clearings only to feed; thus, feeding times are likely to be seriously over-estimated in these studies. The following population-specific socioecological variables were used in this study: maximum group size, average group size, number of adults, number of males, number of females, home range size, day journey length, gorilla density, percentage of food items in diet made of leaves or fruits [%leaves/fruits in diet; note that data on percentage fruit in dung was not included in this analysis as these data might be biased towards high fruit content in the diet (see Rogers *et al.*, 2004)], number of food/fruit species eaten, and density of terrestrial herbaceous vegetation.

For climatic data, we used long-term data as given by the original sources for individual gorilla study sites whenever possible. For those sites that did not provide climate data, we used the Willmott and Matsuura (2001) database. The time period evaluated was 1950–1999 inclusive. For each site for which climate data were required, we calculated average values over those data points in the Willmott and Matsuura dataset that fell within a radius of 0.5° longitude and latitude to the site. Additionally, we used the data from Willmott and Matsuura to compile a dataset containing climate details for the whole of sub-Saharan Africa on a 0.5° longitude and latitude grid. This dataset consists of 11,670 data points evenly distributed across sub-Saharan Africa.

Table 1. Climate data for the 10 gorilla study sites for which information on time budget variables was available

Country	Park	Site	Subsp.	Lat.	Long.	Alt.	P_{ann}	T_{ann}	$P_{mo}SD$	$T_{mo}SD$	$P < 50$
CAR	Dzanga-Ndoki NP	Bai Hokou	*gorilla*	2.83	16.47	440	1633	24.95	71.55	0.67	2.5
CAR	Dzanga-Ndoki NP	Mondika	*gorilla*	2.35	16.27	300	1551	25.20	53.02	0.64	2.5
Congo	Odzala NP	Maya Nord	*gorilla*	0.42	15.00	450	1500	24.33	65.86	0.67	1.75
Congo	Nouabale	Mbeli Bai	*gorilla*	2.25	16.40	480	1430	27.60	53.54	0.67	0.5
Congo	Ndoki	Ndoki	*gorilla*	2.33	16.32	350	1430	24.90	55.03	0.67	0.75
DR Congo	Kahuzi-Biega	Highland	*graueri*	−2.12	28.70	2200	1945	12.40	67.43	0.46	2.5
DR Congo	Virunga	Kabara	*beringei*	−3.63	28.63	3109	1760	19.55	62.91	0.32	1.75
Eq. Guinea	Rio Muni	Rio Muni	*gorilla*	1.75	10.50	600	1796	25.66	197.9	0.76	3.0
Rwanda	Parc des Volcanos	Karisoke	*beringei*	−1.48	29.48	3200	1796	10.90	72.71	0.38	1.0
Uganda	Bwindi Imp. NP	Ruhija	*beringei*	−1.05	29.77	2250	1278	16.05	40.64	0.29	2.5

Note: Lat. = latitude, Long. = longitude, Subsp. = subspecies, Alt. = altitude (m), P_{ann} = mean annual rainfall (mm), T_{ann} = mean annual temperature (°C), $P_{mo}SD$ = standard deviation of monthly rainfall, $T_{mo}SD$ = standard deviation of monthly temperatures, $P < 50$ = number of months with less than 50 mm of rain, CAR = Central African Republic. Data were obtained from various sources, including the references in Table 3 and the Willmott and Matsuura (2001) climate database.

Table 2. Behavioural data for 10 gorilla study sites for which information on time budget variables was available

Country	Site	Bai	Habituated	Max. group size	Average group size	Density	% feed	% rest	% move	# fruit spp.	% fruits
CAR	Bai Hokou	no	semi	18	14.0	1.15	54.5	28.0	13.0	97	63
CAR	Mondika	no	yes	11	11.0	—	42.3	46.66	12.32	70	—
Congo	Maya Nord	yes	yes	—	11.1	—	72.0	—	—	—	—
Congo	Mbeli Bai	yes	no	16	7.69	2.25	67.0	—	—	—	—
Congo	Ndoki	no?	no	10	7.3	2.25	60.2	(27.9)	—	115	—
DR Congo	Highland	no	semi	42	15.48	0.45	45.5	45.1	9.4	24	—
DR Congo	Kabara	no	yes?	27	13.16	0.74	(45.8)	44.8	—	3	—
Eq. Guinea	Okorobiko	no	no?	12	6.77	0.72	48.0	41.7	10.3	54	40
Rwanda	Karisoke	no	yes	28	9.73	1.13	51.47	41.7	6.9	4	—
Uganda	Ruhija	no	yes	31	17.4	0.38	55.0	—	—	30	11

Note: Values in parentheses are estimates (see text for explanation). Bai = bai habitat; % feed/rest/move = percentage of time spent feeding/resting/moving; # fruit spp. = number of fruit species eaten by the gorillas; % fruits = % of food items in the diet made up of fruits. CAR = Central African Republic. For references, see Table 3.

Table 3. References for data in Table 2 and for additional sites (below dashed horizontal line) used for data on population density and diet

Country	Site	Reference(s)
CAR	Bai Hokou	Cipolletta (2003); Doran (1996); Doran and McNeilage (1998); Ganas *et al.* (2004); Goldsmith (1999); Remis (1995, 1997); Remis *et al.* (2001); Yamagiwa *et al.* (2003)
CAR	Mondika	Doran-Sheehy *et al.* (2004); Doran *et al.* (2002), D.M. Doran (personal communication)
Congo	Maya Nord	Yamagiwa *et al.* (2003), www.westerngorilla.org/network/sites.htm
Congo	Mbeli Bai	Doran and McNeilage (1998); Ilambu (2001); Stokes *et al.* (2003), www.westerngorilla.org/network/sites.htm
Congo	Ndoki	Blake *et al.* (1985); Nishihara (1995); Remis (1997); Yamagiwa (1999); Yamagiwa *et al.* (2003)
DR Congo	Highland	Bean (1998); Casimir (1975); Ganas *et al.* (2004); Goodall (1977); Remis (1997); Yamagiwa and Kahekwa (2001); Yamagiwa *et al.* (1992, 1996, 2003)
DR Congo	Kabara	Schaller (1963)
Eq. Guinea	Okorobiko	Jones and Sabater Pi (1971); Remis (1997); Sabater Pi (1977); Sabaterpi (1979); Yamagiwa and Mwanza (1994)
Rwanda	Karisoke	Clutton-Brock (1977); Fossey (1974); Jones and Sabater Pi (1971); Watts (1984, 1988, 1991, 1998); Yamagiwa (1999)
Uganda	Ruhija	Doran and McNeilage (2001); Ganas *et al.* (2004); Robbins (1999); Yamagiwa (1999); Yamagiwa *et al.* (2003)
DR Congo	Fizi-Mwenga	Schaller (1963)
	Itebero	Ganas *et al.* (2004)
	Masisi	Yamagiwa *et al.* (1994)
	Tshibinda	Goodall (1977)
Gabon	Belinga	Tutin and Fernandez (1983)
	Lope	Rijksen (1978); Rogers *et al.* (1992); Tutin *et al.* (1997); Williamson *et al.* (1990)
Uganda	Buhoma	Ganas *et al.* (2004)
	Kayonza	Schaller (1963)

The following climate variables were used in this study: mean annual rainfall in mm (P_{ann}), mean annual mean temperature in °C (T_{ann}), temperature variation between months (calculated as the standard deviation across average values for 12 months: $T_{mo}SD$), rainfall variation between months (measured as the standard deviation across average values for 12 months: $P_{mo}SD$), number of months per year with less than 50 mm of rainfall ($P < 50$), number of months per year with less than 100 mm of rainfall ($P < 100$), and the plant productivity index, P2T [the number of months in the year in which rainfall (in mm) was more than twice the average monthly temperature (Le Houérou, 1984)]. P2T is used as a measure of the growing season in tropical habitats, as it yields a very strong correlation with primary productivity (Le Houérou, 1984), while $P < 50$ and $P < 100$ can be regarded as alternative measures of seasonality. Previous models of primate socioecological systems have shown that these variables can be important components in time budget models (Williamson and Dunbar, 1999; Dunbar, 1992a, 1992b; Hill and Dunbar, 2002; Korstjens *et al.*, 2006; Korstjens and Dunbar, 2007; Lehmann *et al.*, 2007a).

Table 4. Equations used in the model

	Equations	Adj. r^2	*n*	*F*	*P*
Density ($n \cdot \text{km}^{-2}$)	0.023 + 0.00035*alt – 0.21*P < 50 + 0.017*#fruits	0.64	16	10.4	0.001
# fruits	179.742–40.094*ln (%leaves)	0.57	12	13.4	0.004
% leaves	4.109 + 0.024*alt	0.78	6	7.8	0.038
% fruit	100 – %leaves				
Feed	73.226 – 0.016*P_{ann} + 6.16*density	0.87	8	24.1	0.003
Move	10.053 + 0.245*group size – 0.002*alt	0.96	5	48.1	0.02
Rest	33.98 – 0.406*%fruits + 30.168*T_{mo}SD	0.93	5	26.8	0.036
Groom	1.55 + 0.23*group size	Generic equation for Old World Primates (Lehmann *et al.*, 2007b)			

Note: P_{ann} = annual rainfall, P < 50 = number of months with less 50 mm of rain, T_{mo}SD = standard deviation of monthly temperature values, # fruits = number of different fruit species in the diet, % fruits/% leaves = percentage of the diet that consists of fruit/leaves, alt = altitude.

The model

The first step in building the model is to find the set of equations that account for the highest proportion of variance in the three core time budget components (feeding, moving, and resting). We used multiple regression procedures to determine the best-fit multivariate equations for these variables. We assumed that feeding and moving time are each independently determined by climate, diet, and/or group size, and thus did not include them as independent variables in the analysis when either of them was the dependent variable.

In some studies, resting time included essential social time. To correct for this, we calculated the expected social time for each gorilla group using a generic Old World primate equation (see below), and subtracted this from those resting times that included social time. We then used these corrected resting times as a proxy for resting time in the equation-finding process.

We assume that primate social groups will only be able to maintain coherence through time if their members can invest a minimum amount of time in social interaction. We do not specify what form that interaction should take, although in many primate species this will be social grooming. For the purposes of the model, we need to determine how much time gorillas *ought* to spend in social interaction *if* they were to maintain coherent social groups of a size that might be significantly larger than those in which they are typically found. We determined this from a generic linear equation for Old World primates (including gorillas) based on the relationship between mean group size and mean time spent grooming (Lehmann *et al.*, 2007b). Although this equation is a generic equation for all Old World primates, it accurately reflects observed gorilla grooming times (determined by the sizes of groups in which they do habitually live), as is evident from the fact that the residuals for gorillas (standardized residual = 0.08) are well within the range of the average residuals of the whole sample (mean standardized residual = 0 ± 0.95 S.D.).

Once equations for all time budget components were found, we used these equations to calculate the maximum ecologically tolerable group size under various climatic conditions by iteration using a program written in DBase. The model allows group size to increase algorithmically by one individual at a time until the sum of all time budget variables reaches 100. The maximum ecologically tolerable group size for any specific location (or set of climatic conditions) is then defined as the group size of the previous cycle. Because time budget components must have positive values, all equations were constrained to have minimum values of 2% (moving time) and 5% (resting and feeding time) and maximum values of 99%.

Model validation

We validated the model in three ways. First, we tested how accurately the model predicts presence and absence of gorillas at a sample of 254 sites across Africa. This dataset was compiled by screening the primate literature and the Internet, especially the UNEP and WMCM World database (http://sea.unep-wcmc.org/wdbpa/), for protected areas where primates are known to occur. Climate data for these sites were obtained from the Willmott and Matsuura (2001) dataset. To improve statistical independence, only sites separated by at least 0.5° longitude and latitude were included. Sixty-four of the 254 independent sites reported the presence of gorillas. We interpret high predictive power of the model as implying that the underlying equations correctly reflect those variables that limit gorilla distribution. Second, we tested how accurately the model predicts group sizes at sites where gorilla group sizes are known. Since our model is designed to predict *maximum* ecologically tolerable group size, predicted values should be equal to or larger than observed values, depending on whether or not gorillas live near the ecological maximum. Third, we ran a series of sensitivity analyses in which the parameter values in the core equations were varied systematically to determine how sensitive the model output is to errors of parameter estimation. As with all sensitivity analyses, we required the model to be reasonably robust against small changes in parameter estimation, but to perform poorly when parameters are changed drastically: if large-scale changes in parameter values result in a significantly poorer fit of the model, we can assume that the particular set of parameter values included in the model reflects reality.

Statistical analyses

For screening the data and the relations between ecological and time budget variables, we used Pearson correlation analysis as well as bivariate scatter plots (to identify possible non-linear relations). The scatter plots also allowed us to check that the results were not being systematically biased by different levels of habituation of gorilla groups, and to determine whether particular outliers were likely to have a disproportionate influence on equation parameter values. Multivariate regression procedures were then used to obtain equations for each dependent variable of interest (moving, feeding, and resting). Q-Q and P-P plots were used to assess the distribution of residuals, and thereby the validity of using parametric statistics. Collinearity diagnostics were used to control for correlated variables. Finally, we used the time budget equations to calculate the maximum ecologically tolerable group size for each location in the dataset, using the linear program in DBase. The predictive power of the model was determined using χ^2 statistics. Time budget components between sites for which gorilla presence and absence was correctly predicted were compared using independent samples *t*-tests. To compare observed group sizes with those predicted by the model, we used the Wilcoxon Signed Ranks test for related samples (WSR), while predicted group sizes and densities in locations with different forest covers were compared using Mann-Whitney *U*-tests (MWU). We chose non-parametric statistics for these comparisons because we are only interested in the direction of the differences and not in absolute values.

RESULTS

The model

Table 4 lists the equations (summarized schematically in Fig. 1) that were generated by the equation-finding process. Resting time is predicted by temperature variation and the percentage of fruit in the diet. We interpret the first of these as reflecting the impact of heat load (animals are forced to seek shelter and reduce energy expenditure when temperature variation is high), while the second (a negative relationship with percentage of fruit in the diet) suggests a cost to processing leaves (gorillas are hindgut fermenters). The high explanatory power of this equation for observed resting time suggests that gorillas have very little ‘lazy time’ and that most of their resting time is what we termed ‘enforced resting time’ – that is, time that cannot be converted into other core activities as it is determined by diet (digestion) and climate (thermoregulation). Moving time is determined by group size and altitude. Feeding time is primarily affected by population density rather than by group size. In the model, population density is a function of the number of fruit species in the gorilla diet: this gives an average population density for a given habitat, which is then used to calculate feeding time. Neither feeding nor moving time is directly influenced by dietary variables.

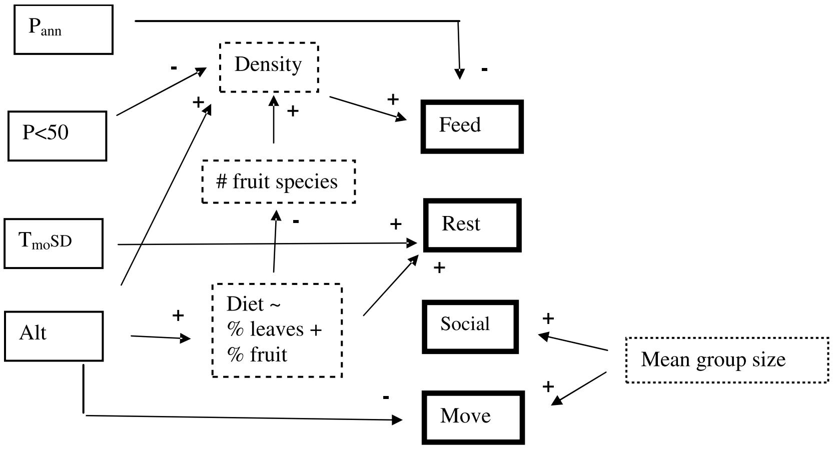

Fig. 1. Flow chart depicting relationships between climate variables and time budget components for gorillas. The arrows depict directional relationships [positive (+) or negative (–) effects] as used in the model. Alt = altitude, P_{ann} = mean annual rainfall, $T_{mo}SD$ = standard deviation of monthly temperatures, $P < 50$ = number of months with less than 50 mm of rain. Variables are classified into climate variables (solid boxes), time budget components (bold boxes), dietary variables (dashed boxes), and demographic variables (dotted boxes).

Model validation

Presence/absence

We calculated the percentage of sites at which presence or absence of gorillas was predicted correctly for the set of 254 African sites where primates are known to occur. With a minimum viable group size of five (the smallest independent group observed in any gorilla population), the model correctly predicted that gorillas would be present at 94% of 64 sites where they were known to be present, and absent from 81% of 190 sites where they were known to be absent (Fig. 2). The number of correct predictions is significantly better than would be expected if presences and absences were assigned at random ($\chi^2 = 119.2$, $n = 254$, d.f. = 1, $P \ll 0.0001$). The majority of the false predictions were false-positives (the model predicts gorillas to be present although they are not known to live at those sites today). This is to be expected, especially because our model does not incorporate geographical barriers that might prevent gorillas from populating specific areas (such as the Congo Basin or West Africa) and does not incorporate more recent effects such as local deforestation. In contrast, a high proportion of false-negatives (sites where gorillas actually live but the model predicts they cannot) would be particularly troubling.

Our definition of a minimum group size of five is simply based on observation. However, we can use the model to determine how realistic this assumption is by calculating model performance for a range of minimum group size values: Table 5 shows that the percentage of correct predictions remains constant across a very wide range of minimum group sizes (up to and including the lower range of observed *mean* group sizes), thus vindicating our choice of five as a minimum viable group size.

Group sizes

We next test whether the model correctly predicted gorilla group sizes. Recall that the model is designed to predict the *maximum* ecologically tolerable group size: observed group sizes should thus all be less than the predicted values. Figure 3 compares observed and predicted group sizes at those sites where gorillas were known to be present. The median of predicted maximum group sizes was 32 (inter-quartile range: 26–43) individuals, while the means of

Table 5. Accuracy (% correct predictions) of the model depending on the minimum cut-off value of predicted group size used for determining the presence or absence of gorillas

	% correct predictions		
Minimum group size (used as cut-off)	Gorillas present ($n = 64$)	Gorillas absent ($n = 190$)	Overall correct ($n = 264$)
1	93.8	78.9	82.7
3	93.8	80.0	83.5
5	93.8	81.1	84.3
7	93.8	82.1	85.0
10	89.1	82.6	84.3

Note: The model is very robust against cut-off value changes, indicating that there are no marginal sites in our dataset.

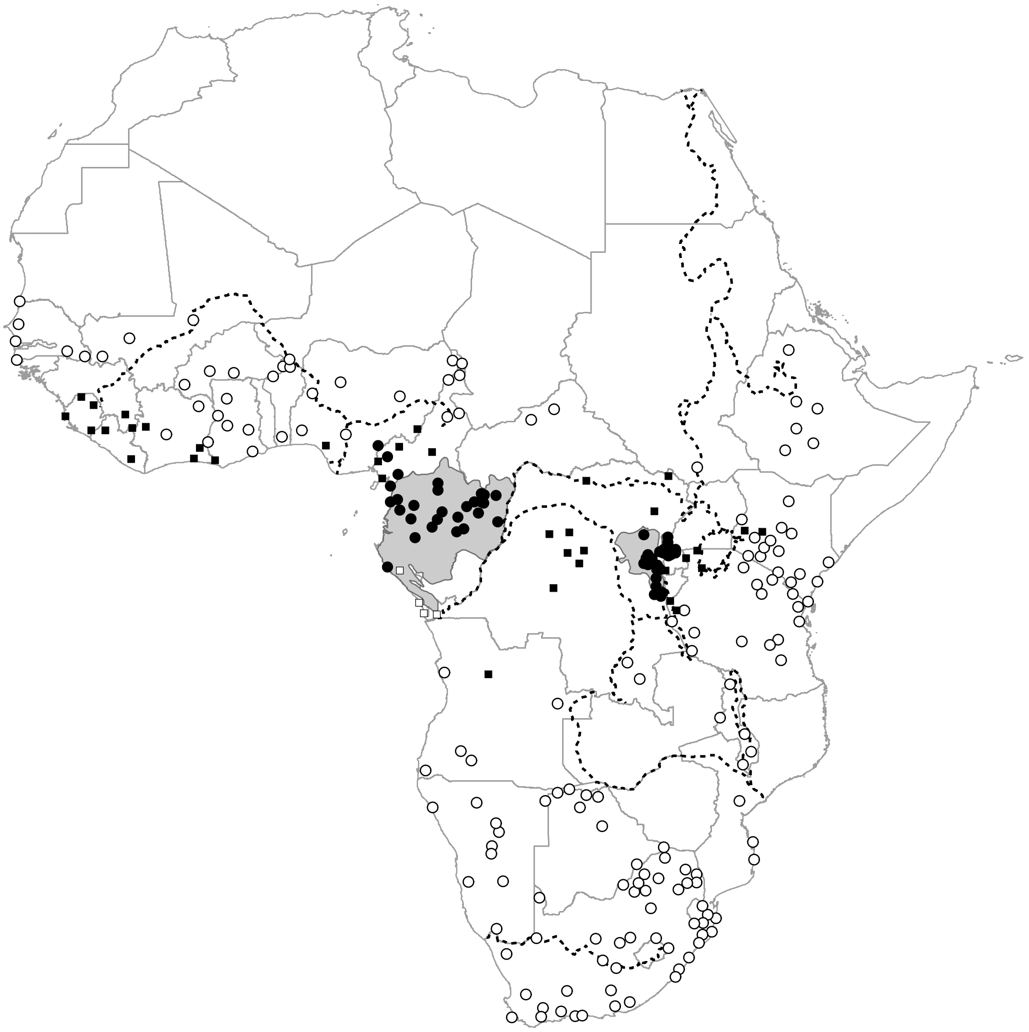

Fig. 2. A test of the model's ability to predict the occurrence of gorillas at a set of 254 sites where gorilla presence or absence is known. ○, correctly predicted absence; ●, correctly predicted presence; ■, falsely predicted presence; and □, falsely predicted absence. In the model, gorillas were defined to be present if predicted group sizes are greater than five individuals. The shaded area depicts the present-day gorilla distribution (the range of the Cross River gorilla population is too small to be depicted on this scale). Dashed lines indicate major rivers.

observed values were 11 (inter-quartile range: 8–16) individuals for average group size ($n = 19$) and 18 ± 13.5 (mean ± S.D.) for maximum group sizes (n = 17). As required by the model, predicted values are, on average, significantly larger than both average and maximum observed values (WSR: $n_{\text{mean}} = 18$, $z_{\text{mean}} = -3.7$, $P_{\text{mean}} < 0.0001$; $n_{\text{max}} = 16$, $z_{\text{max}} = -2.8$, $P_{\text{max}} = 0.003$). Only one of the observed mean group sizes lies above its maximum predicted value, and only four of the observed maximum group sizes do so, and all of these lie very close to the main diagonal (Fig. 3).

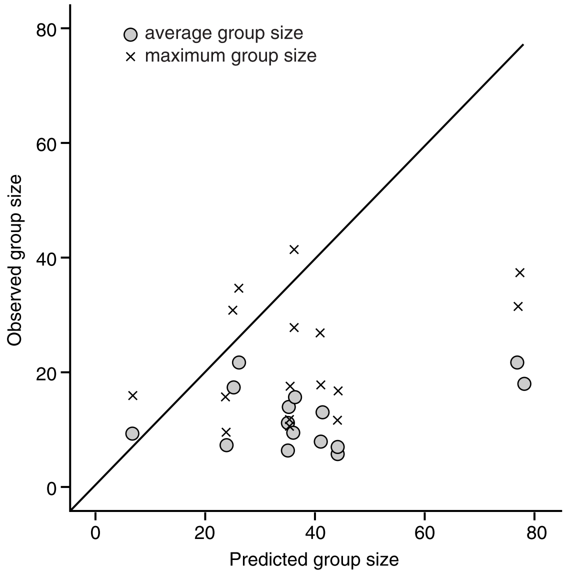

Fig. 3. Observed versus predicted group sizes in gorilla populations. Grey circles represent average observed group sizes, while black crosses represent observed maximum group sizes. All values should lie on or below the main diagonal, the line of equality.

Sensitivity analyses

The slope parameters of the equations were varied one at a time by 15% or 50%. In no case did changing an individual slope parameter by 15% yield a presence/absence distribution that was significantly different from the original model (individual 2×2 χ^2 tests for 19 runs, $P > 0.05$), but, when we changed individual slope parameters by 50%, 14 of 38 sensitivity analyses yielded significantly different distributions. In addition, when we changed all parameter values simultaneously by ±15%, the model produced significantly worse predictions (both 2×2 χ^2 tests with $\chi^2 > 8$ and $P < 0.05$). The model is thus robust to modest errors in the estimation of individual parameter values, but sensitive to larger changes. More importantly, it is very sensitive to the possibility that several parameters might simultaneously incorporate small estimation errors. This suggests that it is the particular set of parameter values we found that is important, thus giving us confidence in the ecological validity of the model.

Gorilla biogeographical distribution

We then used the model to predict the gorillas' distribution in sub-Saharan Africa using a grid of 11,670 coordinates on a 0.5° latitude and longitude lattice derived from the Willmott and Matsuura (2001) climate dataset (see Methods). Figure 4 plots the distribution of suitable gorilla habitat as predicted by the model. While broadly encompassing the current gorilla distribution, the model suggests that gorillas could survive in a wider geographical range than they currently do. In fact, other apes (chimpanzees and bonobos) do live in most of these locations and the model provides a very good fit of the known African great ape distribution. However, in contrast to chimpanzees, which can live in savannah and woodland habitats, all known gorilla populations live in forest with at least 80% tree cover.

Because there is no variation in forest cover between gorilla populations in our dataset, the regression analyses did not include this variable in any of the equations (Table 4). Nonetheless, if we use forest cover [obtained from AVHRR satellite data on forest cover from DeFries *et al.* (2000)] as a secondary filter variable in Fig. 4, predicted gorilla distribution is significantly reduced (dark dots) and gives a much closer fit to the known gorilla distribution.

Fig. 4. Predicted gorilla distribution across Africa based on the model, mapped on a 0.5° latitude × 0.5° longitude grid for the whole of sub-Saharan Africa obtained from Willmott and Matsuura (2001). The predictions are based on group sizes larger than five individuals (defined as the smallest viable maximum ecologically tolerable group size). Light grey circles indicate locations for which the model predicted gorillas to be present with less than 80% forest cover, while darker circles indicate locations for which gorillas were predicted to be present with 80% or more forest coverage (all known gorilla populations live in forests with 80% coverage). Areas left blank indicate areas where the model predicts that gorillas could not live. The dashed lines indicate major rivers.

It is worth noting here that our model predicts significantly smaller group sizes for areas where forest cover is lower than 80% compared with areas where forest cover is above 80% (mean group sizes of 29 and 40, respectively; MWU: $Z_{\text{group size}} = -11.4$, $n = 1338$, $P < 0.0001$), suggesting that gorilla populations would experience greater difficulty surviving in habitats with less than 80% forest cover. In addition, the model also predicts significantly lower gorilla *densities* in habitats with less than 80% forest cover ($z_{\text{density}} = -22$, $n = 1338$, $P < 0.0001$).

Figure 4 suggests that, based on local climatic conditions alone, gorillas could live across Central Africa within the loop of the Congo River, as well as in some West African forests and in some isolated forest patches in south-western Ethiopia. It is likely that these areas all represent suitable habitat for gorillas, but that gorillas never managed to reach these places because of geographical barriers that are well known to limit mammal distributions (notably the Dahomey Gap in West Africa, the Congo River in Central Africa, and the rather arid Rift Valley floor in northern Kenya and southern Sudan).

Time as a limiting factor

Finally, we test the hypothesis that gorilla distribution across sub-Saharan Africa is limited by some aspect of their time budget. Figure 5 shows the median (and range) of predicted percentage of time spent feeding, moving, and resting as predicted by the model for sites where gorillas actually occur (correctly predicted presence) compared with those where they do not (correctly predicted absence). Since some time budget components vary with group size, we restricted this analysis to a constant group size of 10 animals (close to the mean observed group size: see Table 2) so that predicted values can be compared directly. Time budget components for those sites where the model correctly predicts the presence of gorillas ($n = 60$) were well within the range of the actual observed values (predicted mean ± s.d.: feeding time 49.9 ± 9.4; moving time 17.6 ± 5.2; resting time 22.3 ± 6.3; social time 10.5 ± 4.5; for observed values, see Table 2). In contrast, feeding and resting times are significantly higher at sites where gorillas are absent compared with sites where they are present ($\text{feed}_{\text{presence}}$ vs. $\text{feed}_{\text{absence}} = 49.9 \pm 9.4$ vs. 61.7 ± 5.3; $t_{212} = 11.6$, $n = 214$, $P < 0.0001$; $\text{rest}_{\text{presence}}$ vs. $\text{rest}_{\text{absence}} = 22.3 \pm 6.3$ vs. 71.1 ± 24.4; $t_{212} = 15.3$, $n = 214$, $P < 0.0001$), but there is no difference in moving time ($\text{move}_{\text{presence}}$ vs. $\text{move}_{\text{absence}} = 10.5 \pm 1.5$ vs. 10.8 ± 1.3; $t_{202} = 1.4$, $n = 214$, $P = 0.175$). While both feeding and resting times differ significantly between presence and absence sites, the difference in resting time is especially large (about four times higher at sites where gorillas are absent; see Fig. 5). We conclude that the demand for resting time is largely responsible for the absence of gorillas in habitats where they do not occur, and that this in turn is probably a consequence of their being forced to resort to high-leaf diets in more marginal habitats.

DISCUSSION

Time budget models like ours are a first step towards investigating the mechanism by which climatic (environmental) variables limit the biogeographical distribution in a taxon and can even be used when good-quality behavioural and ecological data are limited. It would be easy to criticize our analysis on the grounds that the data from field studies of gorillas are both limited in number and of questionable reliability, due in part at least to the poor observation conditions and shyness of this species. In fact, our results suggest that such a

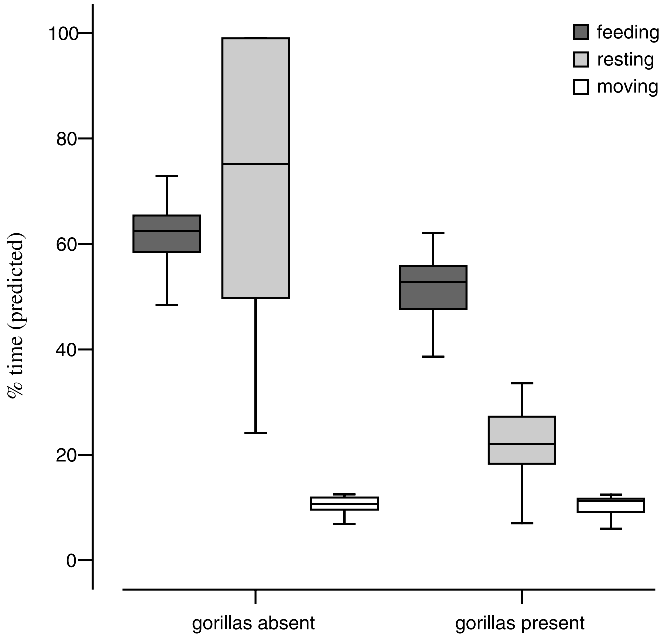

Fig. 5. Time spent feeding, resting, and moving predicted by the model for sites where gorillas are known to be either absent or present. Both feeding and resting time are significantly lower at sites where gorillas live compared with sites where they have not been recorded.

view would be unnecessarily pessimistic. First, irrespective of the quality of the data, the model predicts gorilla biogeographic distribution remarkably accurately (and considerably more accurately than one might expect, given that it is based on *behaviour* and not on more conventional energetics or life tables). Second, and more importantly, the sensitivity analysis confirms that the model is comfortingly robust to modest errors of estimation, providing these are limited to only a single parameter at a time. This encourages us to be more confident in what can be done with the limited datasets that we often have to cope with from field studies of this kind.

Although our model predicts the presence and absence of gorillas remarkably well (Fig. 2), it overestimates the biogeographical distribution of gorillas in some areas, such as the Congo Basin and West Africa (Fig. 4). There are at least three circumstantial reasons why gorillas might not occur in habitats where the model predicts they could.

The first is that gorillas cannot cross major geographical barriers. This would explain why they are restricted to the northern side of the Congo River loop despite the fact that there is suitable habitat south of this river. A similar explanation has been invoked to explain the disjunction between the chimpanzee and bonobo distributions (Wrangham and Peterson, 1997). Elsewhere, other geographical barriers such as savannah stretches or unsuitable forest may have prevented gorillas from colonizing habitats where they could in fact occur (e.g. the coastal forests west of the Dahomey Gap, or Ethiopia east of the Rift Valley). Even if gorillas could occupy these areas, it is clear from Fig. 4 that the size of the habitable area in these cases is quite modest (especially when the forest cover constraint is taken into account): small, fragmented populations generally are at greater risk of extinction due to Allee effects (Cowlishaw and Dunbar, 2000; Stephens and Sutherland, 1999).

Second, chimpanzees and gorillas may not be able to co-exist in marginal habitats, so that the presence of chimpanzees in some of these habitats may have prevented gorillas from living there. Several studies have shown that the diets of gorillas and chimpanzees overlap considerably, and that gorillas tend to become more folivorous, especially during the dry season, in areas where they are in competition with chimpanzees (Tutin *et al.*, 1991, 1997; Tutin and Fernandez, 1993; Yamagiwa *et al.*, 1996). A more folivorous diet would mean more time required for resting, and this is turn would limit their ability to survive in these locations.

Finally, contemporary gorilla distribution is strongly influenced by human activities, such as logging and hunting (e.g. Schaller, 1963; Walsh *et al.*, 2003). However, gorillas must, at some time in the past, have occurred throughout the Democratic Republic of Congo in order to link the western and the eastern subspecies (Kortlandt, 1995). The model thus reinforces the peculiarity of this aspect of gorilla biogeography. It remains unclear, however, why there are no longer any gorillas north of the Congo River between longitudes 19 and 25°E, given the fact that chimpanzees still occupy this area.

Our model also suggests that gorillas do not often live at their ecological maximum (predicted group sizes are at some locations higher than typically observed group sizes), probably because they would not benefit from living in larger groups and the costs of doing so do not outweigh the marginal benefits that accrue. The fact that, ecologically, gorillas *could* live in larger groups thus raises questions about the costs and benefits of sociality for this species.

An important aspect of these models is that we can use them to ask why a species is absent from a particular location. In the case of gorillas, the main problem where gorillas are absent is that required feeding and resting times would be too high to allow individuals to live together in viable groups. Although our taxon-specific model represents a simplification of complex feeding ecology, our results are in line with what has been reported for other primate species: both feeding and resting times appear to be strongly influenced by diet composition – that is, the amount of fruit that can be incorporated into the diet (Dunbar, 1992a; Korstjens and Dunbar 2007). [Note that, even though gorillas are often characterized as being predominantly folivorous, their molar teeth are in fact more similar to those of other frugivorous apes than to those of folivores (Martin, 1990).] Our equations for gorillas also correctly reflect the expected relationships between searching, handling, and processing times of different food types: at sites where gorillas have limited access to suitable fruits (i.e. less forested habitats) and therefore have to ingest more leaves, they have to spend more time resting than at fruit-rich sites (Table 2, Fig. 1). This suggests that processing high-leaf diets is digestively taxing, either because large leaf volume is mechanically limiting (bulk forage results in rapid gut-fill, and animals must wait for the stomach to clear before they can start feeding again) or because leaves impose high digestive costs (due to fermentation). Such a link between digestive capacity, time constraints, and diet choice has been reported in other studies (Schmitz, 1992; Abrams and Schmitz, 1999), indicating that if food choice is sub-optimal, both time and digestive capacity can place strong constraints on species (Klein and Fairall, 1986; Torres-Contreras and Bozinovic, 1997). A high-quality (i.e. fruit-rich) diet, on the other hand, might allow gorillas to live at higher population densities, but it comes at a cost of increased overall feeding time as a result of scramble competition (see also, for example, Watts, 1998). Finally, the model suggests that diet composition affects search time, as reflected in the fact that the degree of frugivory influences moving time (see Fig. 1). Indeed, lowland gorillas (which feed more on fruit) travel further than gorillas in montane habitats (which do not have so many suitable fruiting trees in their habitat) (e.g. Doran and McNeilage, 2001; Yamagiwa *et al.*, 2003;

Doran-Sheehy *et al.*, 2004). In addition, activity (and energy) budgets have been successfully used to predict small-scale habitat and diet choice in, for example, white-tailed deer populations (Schmitz, 1991, 1992). Thus, models like ours show how ecological variables affect individual behaviour and, through this, species biogeography. Although the exact model parameters and variables are necessarily taxon-specific, the overall relationships between climate, time budgets, and biogeography are generally the same (Dunbar, 1992b; Hill, 1999; Korstjens *et al.*, 2006; Korstjens and Dunbar, 2007; Lehmann *et al.*, 2007a).

Taken together, our model provides insights into the mechanisms by which ecological variables influence biogeographical distribution. One benefit of the present model is that it identifies an issue that has hitherto not appeared obvious. In contrast to simple correlation models, our model based on gorilla behaviour (i.e. time budgets) provides us with information about exactly how climatic variables limit the geographical distribution of gorillas. Thus models like these can demonstrate how individual behaviour influences the biogeographical distribution of a species and how behavioural flexibility may help to react to environmental/climatic changes. They thereby go far beyond the limits of the more conventional analyses that relate biogeography or population dynamics directly to climatic or environmental variables.

ACKNOWLEDGEMENTS

J.L. was funded by the British Academy Centenary Research Project; A.H.K. was funded by a grant from the Leverhulme Trust; and R.I.M.D. was supported by a British Academy Research Professorship. We would like to thank Dian Doran-Sheehy who provided us with further details on gorilla time budget data. The in-depth analysis we did would not have been possible without the generosity of Cort Willmott and Kenji Matsuura from the University of Delaware.

REFERENCES

Abrams, P.A. and Schmitz, O.J. 1999. The effect of risk of mortality on the foraging behaviour of animals faced with time and digestive capacity constraints. *Evol. Ecol. Res.*, **1**: 285–301.

Adamczak, V.G. 1999. Variation in the mating system of oribi, *Ourebia ourebi*. PhD thesis, University of Liverpool, Liverpool.

Bean, A.E. 1998. The ecology of sex differences in great ape foraging behaviour and hunter-gatherer subsistence behaviour. PhD thesis, University of Cambridge, Cambridge.

Blake, S., Rogers, E., Fay, J.M., Ngangoue, M. and Ebeke, G. 1985. Swamp gorillas in northern Congo. *Afr. J. Ecol.*, **33**: 285–290.

Casimir, M.J. 1975. Feeding ecology and nutrition of an eastern gorilla group in Mt Kahuzi Region (Republique-Du-Zaire). *Folia Primatol.*, **24**: 81–136.

Cipolletta, C. 2003. Ranging patterns of a western gorilla group during habituation to humans in the Dzanga-Ndoki National Park, Central African Republic. *Int. J. Primatol.*, **24**: 1207–1226.

Clutton-Brock, T.H. 1977. *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. London: Academic Press.

Cowlishaw, G. and Dunbar, R.I.M. 2000. *Primate Conservation Biology*. Chicago, IL: University of Chicago Press.

DeFries, R., Hansen, M., Townshend, J.R.G., Janetos, A.C. and Loveland, T.R. 2000. *Continuous Fields 1 km Tree Cover*. College Park, MD: The Global Land Cover Facility.

Doran, D.M. 1996. Comparative positional behavior in great apes. In *Great Ape Societies* (W.C. McGrew, L. Marchant and T. Nichida, eds.), pp. 213–224. Cambridge: Cambridge University Press.

Doran, D.M. and McNeilage, A. 1998. Gorilla ecology and behavior. *Evol. Anthropol.*, **6**: 120–131.

Doran, D.M. and McNeilage, A. 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In *Mountain Gorillas: Three Decades of Research at Karisoke* (M.M. Robbins, P. Sicotte and K.J. Stewart, eds.), pp. 123–149. New York: Cambridge University Press.

Doran, D.M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P. and Shah, N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *Am. J. Primatol.*, **58**: 91–116.

Doran-Sheehy, D.M., Greer, D., Mongo, P. and Schwindt, D. 2004. Impact of ecological and social factors on ranging in western gorillas. *Am. J. Primatol.*, **64**: 207–222.

du Toit, J.T. and Yetman, C.A. 2005. Effects of body size on the diurnal activity budgets of African browsing ruminants. *Oecologia*, **143**: 317–325.

Dunbar, R.I.M. 1988. *Primate Social Systems*. New York: Cornell University Press.

Dunbar, R.I.M. 1991. Functional significance of social grooming in primates. *Folia Primatol.*, **57**: 121–131.

Dunbar, R.I.M. 1992a. A model of the gelada socioecological system. *Primates*, **33**: 69–83.

Dunbar, R.I.M. 1992b. Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*, **31**: 35–49.

Dunbar, R.I.M. 1996. Determinants of group size in primates: a general model. *Proc. Br. Acad.*, **88**: 33–57.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. and Wessels, K.J. 2002. Vulnerability of South African animal taxa to climate change. *Glob. Change Biol.*, **8**: 679–693.

Fossey, D. 1974. Observations on home range of one group of mountain gorillas (*Gorilla gorilla beringei*). *Anim. Behav.*, **22**: 568–581.

Ganas, J., Robbins, M.M., Nkurunungi, J.B., Kaplin, B.A. and McNeilage, A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Int. J. Primatol.*, **25**: 1043–1072.

Goldsmith, M.L. 1999. Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Int. J. Primatol.*, **20**: 1–23.

Goodall, A.G. 1977. Feeding and ranging behavior of a mountain gorilla group (*Gorilla gorilla beringei*) in the Thibinda-Kahuzi region (Zaire). In *Primate Ecology* (T.H. Clutton-Brock, ed.), pp. 450–479. New York: Academic Press.

Herbers, J.M. 1981. Time resources and laziness in animals. *Oecologia*, **49**: 252–262.

Hill, R.A. 1999. The ecological and demographic determinants of time budgets in baboons: implications for the understanding of cross-populational models of baboon socioecology. PhD thesis, University of Liverpool, Liverpool.

Hill, R.A. and Dunbar, R.I.M. 2002. Climatic determinants of diet and foraging behaviour in baboons. *Evol. Ecol.*, **16**: 579–593.

Ilambu, O. 2001. Ecology of eastern lowland gorilla: is there enough scientific knowledge to mitigate conservation threats associated with extreme disturbances in its distribution range? In *The Apes: Challenges for the 21st Century. Conference Proceedings*, pp. 307–312. Brookfield, IL: Brookfield Zoo.

Jones, C. and Sabater Pi, J. 1971. *Comparative Ecology of Gorilla gorilla (Savage and Wyman) and Pan troglodytes (Blumenbach) in Rio Muni, West Africa*, Vol. 13. Basel: Karger.

Kay, R.F., Madden, R.H., VanSchaik, C. and Higdon, D. 1997. Primate species richness is determined by plant productivity: implications for conservation. *Proc. Natl. Acad. Sci. USA*, **94**: 13023–13027.

Klein, D.R. and Fairall, N. 1986. Comparative foraging behavior and associated energetics of impala and blesbok. *J. Appl. Ecol.*, **23**: 489–502.

Korstjens, A.H. and Dunbar, R.I.M. 2007. Time constraints limit group sizes and distribution in red and black-and-white colobus. *Int. J. Primatol., 28*: 551–575.

Korstjens, A.H., Verhoekx, I.L. and Dunbar, R.I.M. 2006. Time as a constraint on group size in spider monkeys. *Behav. Ecol. Sociobiol.*, **60**: 683–694.

Kortlandt, A. 1995. An ecosystem approach to hominid and ape evolution. In *Human Evolution in its Ecological Context: Paleo-anthropology, Evolution and Ecology of Homo erectus* (J. Bower and S. Sartono, eds.), pp. 87–97. Leiden, Netherlands: Pithecanthropus Centennial Foundation.

Lehmann, J., Korstjens, A.H. and Dunbar, R.I.M. 2007a. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evol. Ecol.*, **21**: 613–634.

Lehmann, J., Korstjens, A.H. and Dunbar, R.I.M. 2007b. Group size, grooming and social cohesion in primates. *Anim. Behav.*, **74**: 1617–1629.

Le Houérou, H.N. 1984. Rain use efficiency – a unifying concept in arid-land ecology. *J. Arid Environ.*, **7**: 213–247.

MacArthur, R.H. and Pianka, E.R. 1966. On the optimal use of a patchy environment. *Am. Nat.*, **100**: 603–609.

Martin, R.D. 1990. *Primate Origins and Evolution*. London: Chapman & Hall.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. and Langvatn, R. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.*, **69**: 959–974.

Nishihara, T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates*, **36**: 151–168.

Post, E. and Forchhammer, M.C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature*, **420**: 168–171.

Remis, M. 1995. Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *Am. J. Phys. Anthropol.*, **97**: 413–433.

Remis, M.J. 1997. Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *Am. J. Primatol.*, **43**: 111–133.

Remis, M.J., Dierenfeld, E.S., Mowry, C.B. and Carroll, R.W. 2001. Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *Int. J. Primatol.*, **22**: 807–839.

Rickleffs, R.E. 1970. *Ecology*. New York: W.H. Freeman.

Rijksen, H.D. 1978. *A Field Study on Sumatran Orang-utans (Pongo pygmaeus abelii): Ecology, Behaviour, and Conservation*. Wageningen, Netherlands: H. Veenmann & Zonen.

Robbins, M.M. 1999. Male mating patterns in wild multimale mountain gorilla groups. *Anim. Behav.*, **57**: 1013–1020.

Rogers, E.M., Maisels, F., Williamson, E.A., Tutin, C.E.G. and Fernandez, M. 1992. Nutritional aspects of gorilla food choice in the Lope Reserve, Gabon. In *Topics in Primatology, Vol. 2: Behavior, Ecology and Conservation* (N. Itoigawa, Y. Sugiyama and G.P. Sackett, eds.), pp. 255–266. Tokyo: University of Tokyo Press.

Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., McFarland, K. *et al.* 2004. Western gorilla diet: a synthesis from six sites. *Am. J. Primatol.*, **64**: 173–192.

Sabater Pi, J. 1977. Contribution to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea (West Africa). *Primates*, **18**: 183–204.

Sabaterpi, J. 1979. Feeding behavior and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). *Zeitschrift für Tierpsychol.: J. Compar. Ethol.*, **50**: 265–281.

Schaller, G.B. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago, IL: University of Chicago Press.

Schmitz, O.J. 1991. Thermal constraints and optimazation of winter feeding and habitat choice in white-tailed deer. *Holarctic Ecol.*, **14**: 104–111.

Schmitz, O.J. 1992. Optimal diet selection by white-tailed deer – balancing reproduction with starvation risk. *Evol. Ecol.*, **6**: 125–141.

Sergio, F. 2003. From individual behaviour to population pattern: weather-dependent foraging and breeding performance in black kites. *Anim. Behav.*, **66**: 1109–1117.

Stelzner, J.K. 1988. Thermal effects on movement patterns of yellow baboons. *Primates*, **29**: 91–105.

Stephens, P.A. and Sutherland, W.J. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.*, **14**: 401–405.

Stokes, E.J., Parnell, R.J. and Olejniczak, C. 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav. Ecol. Sociobiol.*, **54**: 329–339.

Torres-Contreras, H. and Bozinovic, F. 1997. Food selection in an herbivorous rodent: balancing nutrition with thermoregulation. *Ecology*, **78**: 2230–2237.

Turner, W.C., Jolles, A.E. and Owen-Smith, N. 2005. Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*). *J. Zool.*, **267**: 291–299.

Tutin, C.E.G. and Fernandez, M. 1983. Gorillas feeding on termites in Gabon, West Africa. *J. Mammal.*, **64**: 530–531.

Tutin, C.E.G. and Fernandez, M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lope Reserve, Gabon. *Am. J. Primatol.*, **30**: 195–211.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E.A. and McGrew, W.C. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Phil. Trans. R. Soc. Lond. B*, **334**: 179–186.

Tutin, C.E.G., Ham, R.M., White, L.J.T. and Harrison, M.J.S. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *Am. J. Primatol.*, **42**: 1–24.

van Soest, P.J. 1982. *Nutritional Ecology of the Ruminants*. Ithaca, NY: Cornell University Press.

Walsh, P.D., Abernethy, K.A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M.E. *et al.* 2003. Catastrophic ape decline in western equatorial Africa. *Nature*, **422**: 611–614.

Watts, D. 1988. Environmental influences on mountain gorilla time budgets. *Am. J. Primatol.*, **15**: 195–211.

Watts, D.P. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *Am. J. Primatol.*, **7**: 323–356.

Watts, D.P. 1991. Strategies of habitat use by mountain gorillas. *Folia Primatol.*, **56**: 1–16.

Watts, D.P. 1998. Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 1. Consistency, variation, and home range size and stability. *Int. J. Primatol.*, **19**: 651–679.

Williamson, D. and Dunbar, R.I.M. 1999. Energetics, time budgets and group size. In *Comparative Primate Socioecology* (P.C. Lee, ed.), pp. 320–338. Cambridge: Cambridge University Press.

Williamson, E.A., Tutin, C.E.G., Rogers, M.E. and Fernandez, M. 1990. Composition of the diet of lowland gorillas at Lope in Gabon. *Am. J. Primatol.*, **21**: 265–277.

Willmott, C.J. and Matsuura, K. 2001. *Terrestrial air temperature and precipitation: monthly and annual climatologies* (Version 3.02). Available at: http://climate.geog.udel.edu/≈climate/).

Wirtz, P. and Oldekop, G. 1991. Time budgets of waterbuck (*Kobus ellipsiprymnus*) of different age, sex and social status. *Zeitschrift für Saugetierkunde: Int. J. Mammal. Biol.*, **56**: 48–58.

Wrangham, R.J. and Peterson, D. 1997. *Demonic Males: Apes and the Origins of Human Violence*. London: Bloomsbury.

Yamagiwa, J. 1999. Socioecological factors influencing population structure of gorillas and chimpanzees. *Primates*, **40**: 87–104.

Yamagiwa, J. and Kahekwa, J. 2001. Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In *Mountain Gorillas: Three Decades of Research in Karisoke* (M.M. Robbins, P. Sicotte and K.J. Stewart, eds.), pp. 89–122. New York: Cambridge University Press.

Yamagiwa, J. and Mwanza, N. 1994. Day journey length and daily diet of solitary male gorillas in lowland and highland habitats. *Int. J. Primatol.*, **15**: 207–224.

Yamagiwa, J., Mwanza, N., Yumoto, T. and Maruhashi, T. 1992. Travel distances and food habits of eastern lowland gorillas: a comparative analysis. In *Topics in Primatology, Vol. 2: Behavior, Ecology and Conservation* (N. Itoigawa, Y. Sugiyama and G.P. Sackett, eds.), pp. 267–281. Tokyo: University of Tokyo Press.

Yamagiwa, J., Mwanza, N., Yumoto, T. and Maruhashi, T. 1994. Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates*, **35**: 1–14.

Yamagiwa, J., Maruhashi, T., Yumoto, T. and Mwana, N. 1996. *Dietary and Ranging Overlap in Sympatric Gorillas and Chimpanzees in Kahuzi-Biega National Park, Zaire*. Cambridge: Cambridge University Press.

Yamagiwa, J., Kahekwa, J. and Basabose, A.K. 2003. Intra-specific variation in social organization of gorillas: implications for their social evolution. *Primates*, **44**: 359–369.