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ORIGINAL ARTICLE

A critical assessment of two species distribution models: a case study of the vervet monkey (*Cercopithecus aethiops*)

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ABSTRACT

Aim Species distribution models are invaluable tools in biogeographical, ecological and applied biological research, but specific concerns have been raised in relation to different modelling techniques in terms of their validity. Here we compare two fundamentally different approaches to species distribution modelling, one based on simple occurrence data where the lack of an ecological framework has been criticized, and the other firmly based in socio-ecological theory but requiring highly detailed behavioural information that is often limited in availability.

Location (Sub-Saharan) Africa.

Methods We used two distinct techniques to predict the realized distribution of a model species, the vervet monkey (*Cercopithecus aethiops* Linnaeus, 1758). A maximum entropy model was produced taking 13 environmental variables and presence-only data from 174 sites throughout Africa as input, with an additional 58 sites retained to test the model. A time-budget model considering the same environmental variables was constructed from detailed behavioural data on 20 groups representing 14 populations, with presence-only data from the remaining 218 sites reserved to test model predictions on vervet monkey occurrence. Both models were further validated against a reference species distribution map as drawn up by the African Mammals Databank.

Results Both models performed well, with the time budget and maximum entropy algorithms correctly predicting vervet monkey presence at 78.4% and 91.4% of their respective test sites. Similarly, the time-budget model correctly predicted presence and absence at 87.4% of map pixels against the reference distribution map, and the maximum entropy model achieved a success rate of 81.8%. Finally, there was a high level of agreement (81.6%) between the presence–absence maps produced by the two models, and the environmental variables identified as most strongly driving vervet monkey distribution were the same in both models.

Main conclusions The time-budget and maximum entropy models produced accurate and remarkably similar species distribution maps, despite fundamental differences in their conceptual and methodological approaches. Such strong convergence not only provides support for the credibility of current results, but also relieves concerns about the validity of the two modelling approaches.

Keywords

Africa, Cercopithecidae, *Cercopithecus aethiops*, maximum entropy model, NDVI, species distribution modelling, time budget model, vervet monkey.

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INTRODUCTION

Investigations into the geographical ranges and distributions of species feature prominently within the ecological and biogeographical literature. Although the motivation for these enquiries has varied from ecological (Buermann *et al.*, 2008) and evolutionary (Graham *et al.*, 2004) to conservation (Wilson *et al.*, 2005) and climate-change-related (Thomas *et al.*, 2004) topics, the vast majority of studies rely on a form of environmental niche modelling that relates simple species occurrence data (i.e. information on presence–absence or presence-only) to spatial information on selected environmental conditions. This straightforward and intuitive approach has proved very successful and offers a powerful predictive tool to assess the past, current and future distributions of species. Consequently, this correlative approach to species distribution modelling has found broad application in both fundamental and applied ecological research (Guisan & Zimmermann, 2000) and has greatly contributed to a 'more rigorously scientific, more informative and more useful ecology' (Peters, 1991, p. 274).

In constructing species distribution models on the basis of simple occurrence data, a distinction has been made between three essential model components (Austin, 2002): (1) an ecological model, concerned with the conceptual knowledge, assumptions and ecological theory underlying the distribution of a species; (2) a data model, comprising an effective data collection strategy; and (3) a statistical model, establishing the quantitative link between occurrence and local environment. Driven by the rapid advances in the availability and quality of spatially explicit environmental data (Kerr & Ostrovsky, 2003; Turner *et al.*, 2003; Kozak *et al.*, 2008) as well as in the plethora of statistical techniques available (Segurado & Araújo, 2004; Elith *et al.*, 2006; Hernandez *et al.*, 2006), the focus in recent studies has been overwhelmingly methodological. This emphasis on the data and statistical component models has come at the expense of a full integration of ecological theory into correlative species distribution modelling and may have undermined the validity of the approach (Guisan & Thuiller, 2005; Austin, 2007).

In contrast to a reliance on simple occurrence data, primatologists have typically used highly detailed behavioural data to model the distribution of their study subjects (e.g. Dunbar, 1992, 1996). The latest generation of these models project predictions into geographical rather than (hyper-dimensional) ecological space (Korstjens *et al.*, 2006; Korstjens & Dunbar, 2007; Lehmann *et al.*, 2007, 2008), generating readily interpretable maps of the predicted range of occurrence. The framework behind this radically different approach to species distribution modelling is firmly rooted in socio-ecological theory and exploits the relationship between time allocation, group size and local ecological conditions. It starts from the premise that time is an important resource affecting animal activity and, as is true for most resources, is usually limited. To maximize inclusive fitness, animals must thus adaptively allocate their time over functionally distinct behaviours (Pulliam, 1973; Caraco, 1979a,b; Pulliam & Caraco, 1984). For primates living in social groups this entails that time has to be divided over four main time budget components (feeding, moving, social interactions and resting: Dunbar, 1992, 1996) to meet nutritional, thermoregulatory and social demands, whilst avoiding predation (Schoener, 1971; Mangel & Clark, 1986; Mitchell & Lima, 2002). As local time budget demands are governed by the social (i.e. group size) and ecological environment, time constraints conversely impose a limit on the maximum sustainable group size under a given ecological regime. Ultimately, this species-specific maximum sustainable group size also relates to a taxon's ability to occur. The time budget approach to predicting the geographical distribution of a species has found wide application within primatology, but not elsewhere.

Here we present a long-overdue comparison between the time budget model and a correlative species distribution model based on simple occurrence data, using the widely studied vervet monkey (*Cercopithecus aethiops* Linnaeus, 1758) as our model species. In doing so, we fully integrate the time budget approach (Dunbar, 1992, 1996) into the powerful modelling environment of a Geographical Information System (GIS), which not only greatly facilitates model evaluation, but also allows straightforward comparison to other species distribution models. As a comparator model we selected an easily implemented algorithm based on presence-only data: Maxent (Phillips *et al.*, 2004, 2006; Phillips & Dudík, 2008). Based on maximum entropy modelling, this algorithm has been found to produce highly accurate predictions over a wide range of species and geographical regions (Elith *et al.*, 2006; Hernandez *et al.*, 2006). In two important respects though, the time budget and maximum entropy models lie at opposite ends of the species distribution modelling spectrum. First, whereas the time budget model is firmly rooted in ecological theory, the maximum entropy model originates from statistical mechanics and machine-learning principles and does not necessarily achieve prediction on an ecological process basis. Second, the time budget model puts extremely high demands on its input (detailed behavioural data) and is consequently limited in its scope and applicability, whereas the maximum entropy model merely requires readily available presence-only data and is easily applied to a broad range of taxa. A direct comparison of these two species distribution models should, then, yield interesting insights into the strengths and weaknesses of both techniques.

MATERIALS AND METHODS

Study species and collection of animal data

The vervet monkey (*Cercopithecus aethiops*) is an opportunistic omnivorous primate with a flexible behavioural repertoire, which enables it to occur throughout most of sub-Saharan Africa (although it is generally absent from deserts and tropical rainforests: Willems, 2007). Animals are active during daylight hours and maintain a semi-terrestrial semi-arboreal lifestyle, which, combined with a relatively small body size (males: 4–8 kg; females 3–5 kg), renders them susceptible to predation by a wide range of mammalian, avian and reptilian predators (Enstam & Isbell, 2007; Willems & Hill, 2009). Multi-male multi-female groups, typically of around 20 individuals, occupy stable home ranges that may overlap to varying degrees and readily habituate to human observers, thereby allowing the collection of detailed data on key socio-ecological parameters and processes.

Information on group size, time allocation, range use and diet was collected from as many localities throughout sub-Saharan Africa as possible. Behavioural data were collated in an extensive literature review and complemented with kind donations of unpublished records (see Acknowledgements). In total, information on at least group size was available from an estimated 182 groups, representing 36 populations. In addition, information on the documented presence of vervet monkeys was gathered for another 196 sites (Hill *et al.*, 2007), yielding a total of 232 localities of known occurrence. A reference species distribution map against which to assess the predictions of both models was taken from the African Mammals Databank (IEA, 1998a,b). This map was deemed the most accurate distribution map available for vervet monkeys and agreed with 218 out of the 232 sites of known occurrence (94.0%).

Environmental data

Climatic information over the whole of Africa was extracted from the spatially interpolated dataset developed by Hijmans *et al.* (2005). In addition, climatic variables of particular interest to primate socio-ecology (see Bronikowski & Webb, 1996, and Williamson & Dunbar, 1999) were calculated, as was the annual range in local day length (Hill *et al.*, 2003). Information on primary productivity was obtained from the remotely sensed Normalized Difference Vegetation Index (NDVI), a well-established spectral correlate of photosynthetic activity (e.g. Kerr & Ostrovsky, 2003). NDVI data used in this study stemmed from the Advanced Very High Resolution Radiometer (AVHRR; Cracknell, 2001) and were processed into an 8-km decadal time-series for the entire African continent by the GIMMS-group at NASA's Goddard Space Flight Centre (Tucker *et al.*, 2005). Monthly maximum value composites (Holben, 1986) were constructed to further minimize the effects of atmospheric and topographic contaminations. From these, annual maximum and minimum NDVI composites were computed. A total of 13 environmental variables thus served as input for the two species distribution models. Of these, five related to temperature [annual mean (T_{mean}), minimum of coldest month (T_{min}), maximum of warmest month (T_{max}), seasonality (standard deviation; T_{SD}), and mean diurnal range ($T_{daily\ range}$)], four to precipitation [annual total (P_{annual}), total of driest month ($P_{dry\ month}$), total of wettest month ($P_{wet\ month}$) and rainfall seasonality (Shannon's index of evenness; $P_{H'}$)], three to primary productivity [NDVI of the most productive month ($NDVI_{max}$), NDVI of the least productive month ($NDVI_{min}$), number of months in which total precipitation (in mm) exceeds twice the monthly average temperature (in °C) ($P > 2T$, which equates to the length of the growing season: Le Houérou, 1984)], and one to seasonality in photoperiod (annual range in day length, Day $length_{range}$).

Parameterization of the time budget model

Sufficiently detailed information to develop the time budget model was available for up to 20 groups, representing 14 populations (Table 1). Multiple-regression analyses were conducted to obtain best-fit equations for the four main time budget components. However, because best-fit equations are simplistic mathematical abstractions of a complex socio-ecological phenomenon, they must be interpreted with care and sound biological reasoning. Most notably, where model predictions suggest that the external environment poses very low time allocation demands on individual time budget components (e.g. feeding), real animals may have to dedicate a larger amount of time than predicted because of internal demands (e.g. sufficient nutrient acquisition). Conversely, the maximum amount of time that animals can realistically allocate to each behavioural component will be much less than 100% owing to both physiological or social limitations and the time allocation demands of other time budget components. To estimate the maximum ecologically, rather than mathematically, sustainable group size, a minimum value equal to the observed minimum in the behavioural dataset was therefore imposed on the predicted time allocation demands of all time budget components. Similarly, where predicted time allocation demands exceeded the respective empirically observed maxima, it was assumed that the monkeys could not meet local demands. Statistically, these imposed biological cut-off values (Table 2) implied that predictions of the best-fit equations were constrained to the empirically observed domain of all individual time budget components (i.e. no extrapolation). Moreover, for vervet monkeys to be able to occur, the local sum of the four time budget components cannot exceed 100%. Estimating the maximum ecologically sustainable group size thereby inherently yields a biologically informed presence–absence map.

Parameterization of the maximum entropy model

The maximum entropy algorithm, as applied to species distribution modelling, aims to calculate the unknown distribution of a species over a geographical region of interest from a sample set of locations of known occurrence and spatially explicit environmental conditions. It does so by calculating the distribution of maximum entropy (i.e. closest to uniform), subject to the constraint that expected values of the environmental conditions (or fitted functions thereof) under this estimated distribution match their empirically observed average (Phillips *et al.*, 2004, 2006). In Bayesian terms this is equivalent to maximizing the likelihood of the predicted

Table 1 The 14 populations of vervet monkey (*Cercopithecus aethiops*) throughout Africa for which sufficiently detailed time allocation data were available to parameterize the time budget model. Presented figures are population averages if information was available for more than one group.

					Time allocation (%)				Range use		Diet (%)					
Site	Country	Lat.	Long.	Group size	Feed	Move	Social	Rest	DJL (m)	HR (ha)	Fruit	Seed	Flower	Leaves	Animal	Main references
Amboseli	Kenya	−2.40	37.17	15.6	35.4	14.3	13.6	36.8	–	27.3	11.5	24.9	14.9	22.5	7.7	(Struhsaker, 1967; L. Isbell, unpublished data)
Badi	Senegal	13.17	−13.25	11.4	13.0	17.0	13.0	57.0	550	20	–	–	–	–	–	(Dunbar, 1974)
Bandiala	Senegal	13.65	−16.55	33.0	8.1	20.6	7.6	63.7	–	138	–	–	–	–	–	(Galat & Galat-Luong, 1976)
Blydeberg	South Africa	−24.43	30.77	33.0	42.0	15.0	26.0	17.0	–	77	48.9	18.4	1.4	1.4	3.9	(Barrett, 2005)
Bole Valley	Ethiopia	9.42	38.00	18.8	28.0	28.9	11.4	31.8	700	30	–	–	17.6	18.7	7.4	(Dunbar & Dunbar, 1974)
Entebbe	Uganda	0.60	32.45	21.0	19.7	12.5	17.2	50.6	596	12	–	–	–	–	–	(Saj, 1998)
Kalamaloue	Cameroon	12.15	14.88	47.3	23.4	19.8	5.0	49.9	1429.4	94.6	59.5	9.5	10.1	12.9	6.6	(Kavanagh, 1977; Nakagawa, 2000 & unpublished data)
Lajuma	South Africa	−23.04	29.43	17.8	42.8	21.7	9.8	25.7	1580.7	114.1	51	25	0.9	14.5	0.3	(Willems, 2007)
Mt Assirik	Senegal	12.88	−12.77	25.5	–	–	8.5	46.7	1515	178.4	50	13	13	7	13	(Harrison, 1983a,b, 1985)
N'Dioum	Senegal	16.55	−14.78	39.5	27.0	41.0	7.0	25.0	–	–	26.6	–	2.7	37.1	13.1	(Galat & Galat-Luong, 1977)
Old Oyo	Nigeria	8.97	4.30	20.0	52.7	30.2	7.5	9.7	–	–	–	–	–	–	–	(Adeyemo, 1997)
Samburu-Isiolo	Kenya	−2.56	37.50	32.7	37.5	12.2	–	–	1500	81	7.8	24.9	49.9	16.6	0.8	(Whitten, 1982; P.L. Whitten, unpublished data)
Segera, Laikipia	Kenya	0.25	36.83	17.5	23.8	11.7	15.9	48.6	1328.5	25	4.4	8.4	4.9	3	2.9	(Enstam & Isbell, 2007; L. Isbell, unpublished data)
Windy Ridge	South Africa	−28.58	31.77	23.0	32.8	21.2	22.6	23.4	–	–	–	–	–	–	–	(Baldellou, 1991)

DJL, day journey length; HR, home range.

Table 2 Biological cut-off values imposed on the behavioural categories in the time budget model of vervet monkey (*Cercopithecus aethiops*) distribution. Note that the maximum value for moving time was chosen more conservatively than suggested by its empirically observed range. This was motivated by starvation-related deaths in the population for which the figure of 41.0% was reported (Galat & Galat-Luong, 1977), which strongly suggests that the animals' time budget in this study was not at a sustainable equilibrium with its environment.

Time budget component	Observed range (%)	Cut-off value (%)	
Feeding	8.1–52.7	10–55	Σ100%
Moving	11.7–41.0	10–35	
Social	5.0–26.0	5–25	
Resting	9.7–63.7	10–65	

probability of distribution, given the information at hand. Conceptually, maximum entropy modelling bears a strong resemblance to other statistical techniques commonly used in species distribution modelling, most specifically generalized linear and additive models (GLMs and GAMs). The algorithm was trained on 75% of all locations of known vervet monkey occurrence, reserving a random 25% of sites to assess model performance ($n_{\text{training}} = 174$; $n_{\text{test}} = 58$). Because occurrence records never fell within the same pixel and the mean distance between each test locality and its nearest training site was greater than 100 km (mean ± SE = 112.1 km ± 12.9), spatial autocorrelation within the data was unlikely to be a significant concern.

The model considered linear, quadratic, product, threshold, hinged and discrete functions of all environmental predictors, allowing maximum flexibility (Phillips & Dudík, 2008). The relative importance of all environmental variables in the model was assessed using jackknife re-sampling, and a logistic habitat suitability map was generated to reflect the estimated probability of occurrence. A binary presence–absence map was produced from this by taking the balance threshold (at which the model's intrinsic omission rate is balanced against its fractional predicted area: Phillips *et al.*, 2006) as a cut-off point to demarcate the predicted extent of occurrence. This mode of thresholding (see also Buermann *et al.*, 2008) was deemed most appropriate in the current exercise given: (1) the predicted values assigned to training sites (i.e. the intrinsic omission rate); (2) the relatively large number of occurrence localities; and (3) the context in which the resulting binary distribution map was to be used (to estimate the realized rather than the potential distribution). Model parameters, lastly, were optimized to predict the realized distribution (following Phillips & Dudík, 2008).

GIS environment and statistical analysis

All variables were incorporated into a Geographical Information System (GIS, ArcGIS Desktop 9.0 and Idrisi Andes: ESRI, 2004; Eastmann, 2006), which served as the modelling environment within which to develop and validate both models. Prior to model parameterization and analyses, data were re-sampled to a common pixel size of 8 km and projected into the Albers Equal Area Conic coordinate system for Africa.

Ensuing model predictions were validated in three distinct ways. First, success rates at correctly predicting vervet monkey presence were evaluated at a number of independent test sites ($n_{\text{time budget}} = 218$; $n_{\text{maximum entropy}} = 58$). Second, the degree of similarity between the two predicted extents of occurrence and the reference species distribution map was assessed. For this purpose, a spatial adaptation of Cohen's kappa index of agreement (κ_{no}: Pontius, 2000, 2002) was computed. Third, the predicted maximum ecologically tolerable group size of the time budget model was compared with the observed maximum group size in the 36 populations for which empirical counts on group size were available. For the habitat suitability map produced by the maximum entropy model, correlations were sought with behavioural variables available from these populations. In addition to the three tests of biological validity and information content of both models, the degree of similarity between the two methods was established.

Statistical analyses were conducted in the spss 15.0 (SPSS, Inc., 2006), Maxent 3.2.1 (Phillips *et al.*, 2006; Phillips & Dudík, 2008), Idrisi Andes (Eastmann, 2006) and R 2.7.2 (R Development Core Team, 2008) software packages.

RESULTS

Time budget model

Best-fit equations for the main time budget components are presented in Table 3. Because the amount of time that animals spent moving was best predicted by the proportion of leaves in the local diet, a best-fit equation for this variable was calculated as well. Regression plots were examined, and diagnostics to assess the accuracy and generalizability of the equations can be found in Appendix S1 in the Supporting Information. A schematic flowchart of the time budget model is depicted in Fig. 1. Implementation in the GIS generated time allocation demands as predicted over the whole of Africa (Fig. 2). Note that local demands on resting time could not be determined directly owing to the inclusion of group size as an unknown predictor variable. Instead, the proportion of time available for resting (consisting of both resting time demands and an unknown surplus of time) was calculated by subtracting the sum of local demands of the three other time budget components from 100%. Finally, maximum ecologically tolerable group size, the group size at which all uncommitted resting time has been re-allocated to other time budget components, was calculated as well (Fig. 3a). This was done by setting resting time demands to the biologically determined minimum cut-off value of 10% and subsequently rewriting the resting time equation from Table 3 as:

Table 3 Parameter estimates and key statistics of the regression analyses performed to quantify the relationship between local ecological conditions, group size and time allocation within the time budget model for vervet monkey (*Cercopithecus aethiops*) distribution throughout Africa. The proportion of leaves in the local diet was found to be the most significant predictor of moving time and was therefore expressed as a function of environmental conditions as well.

	B	SE_B	β	$t_{(\beta = 0)}$	F	SE_{model}	$R^2_{Adj.}$
Feeding Intercept	−78.76	13.59		−5.80***	17.14***	6.85	0.843
$P_{H'}$	130.60	17.52	1.39	7.46***			
$NDVI_{min}$	−104.32	17.13	−1.35	−6.09***			
T_{SD}	0.96	0.16	0.89	5.95***			
P_{annual}	0.03	0.01	0.69	3.69**			
Moving Intercept	10.22	3.52		2.90**	16.12**	5.63	0.716
Leaves	0.76	0.19	0.87	4.02**			
Social Intercept	−24.86	10.85		−2.29**	9.40***	3.62	0.677
P > 2T	1.87	0.38	0.96	4.99***			
$T_{daily\ range}$	1.65	0.67	0.47	2.45**			
Day $length_{range}$	2.09	0.94	0.37	2.22*			
Resting Intercept	84.60	6.87		12.31***	36.28***	6.34	0.865
Feeding	−1.24	0.15	−0.92	−8.31***			
Group size	−0.52	0.21	−0.28	−2.47**			
Leaves Intercept	51.74	9.48		5.46***	15.25***	8.63	0.704
$NDVI_{min}$	−111.96	25.49	−0.69	−4.39***			
$P_{dry\ month}$	0.81	0.21	0.60	3.82***			

$P_{H'}$, rainfall seasonality (Shannon's index of evenness); $NDVI_{min}$, NDVI of the least productive month; T_{SD}, temperature seasonality (standard deviation); P_{annual}, annual total precipitation; P > 2T, length of growing season; $T_{daily\ range}$, mean diurnal temperature range; Day $length_{range}$, annual range in day length; $P_{dry\ month}$, total precipitation of the driest month.
$^*P < 0.10$, $^{**}P < 0.05$, $^{***}P < 0.01$.

$$\begin{aligned}\text{Group size} &= \frac{84.60 - \text{Resting} - 1.24\,\text{Feeding}}{0.52} \Rightarrow \\ &= \frac{74.60 - 1.24\,\text{Feeding}}{0.52}.\end{aligned}$$

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Maximum entropy model

Performance of the maximum entropy algorithm was assessed by both threshold-independent and threshold-dependent procedures. The importance of environmental variables in the maximum entropy model as assessed by jackknife re-sampling is presented in Fig. 4. Outcomes of the internal (threshold-independent) evaluation of the model and model response curves can be found in Appendix S2. Habitat suitability within the extent of occurrence as demarcated by the balance threshold (calculated at 0.105) is given in Fig. 3(b).

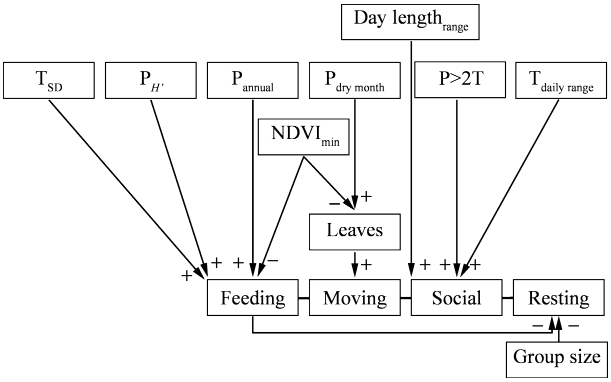

Figure 1 Flowchart of the time budget model of vervet monkey (*Cercopithecus aethiops*) distribution, depicting the inferred causal relationships between climatic conditions, primary productivity, dietary components, time allocation and group size. Day $length_{range}$, annual range in day length; T_{SD}, temperature seasonality (standard deviation); $P_{H'}$, rainfall seasonality (Shannon's index of evenness); P_{annual}, annual total precipitation; $P_{dry\ month}$, total precipitation of the driest month; P > 2T, length of growing season; $T_{daily\ range}$, mean diurnal temperature range; $NDVI_{min}$, NDVI of the least productive month.

Performance and comparison of models

The time budget model correctly predicted vervet monkey presence at 171 out of 218 independent test sites (78.4%), whereas the maximum entropy model at its balance threshold gave correct predictions for 53 out of 58 independent test sites (91.4%). Both models performed significantly better than random (exact binomial test: $P < 0.001$, in both cases), but, because of overlapping 95% confidence intervals around the respective success rates, nothing conclusive could be deduced from this initial examination about relative model performance.

A second, more demanding, test was subsequently conducted by establishing the degree of similarity between the modelled extents of occurrence and the reference species distribution map (Fig. 5a,b). In this test scenario, the time budget model correctly predicted vervet monkey presence and absence for 87.4% of all map pixels whereas the maximum entropy model had a success rate of 81.8%. Overall performance as indexed by κ_{no} was also higher for the time budget model ($\kappa_{no} = 0.749$) than for the maximum entropy model ($\kappa_{no} = 0.636$).

Third, maximum ecologically sustainable group size as predicted by the time budget model was compared with the observed maximum group size in 36 populations for which

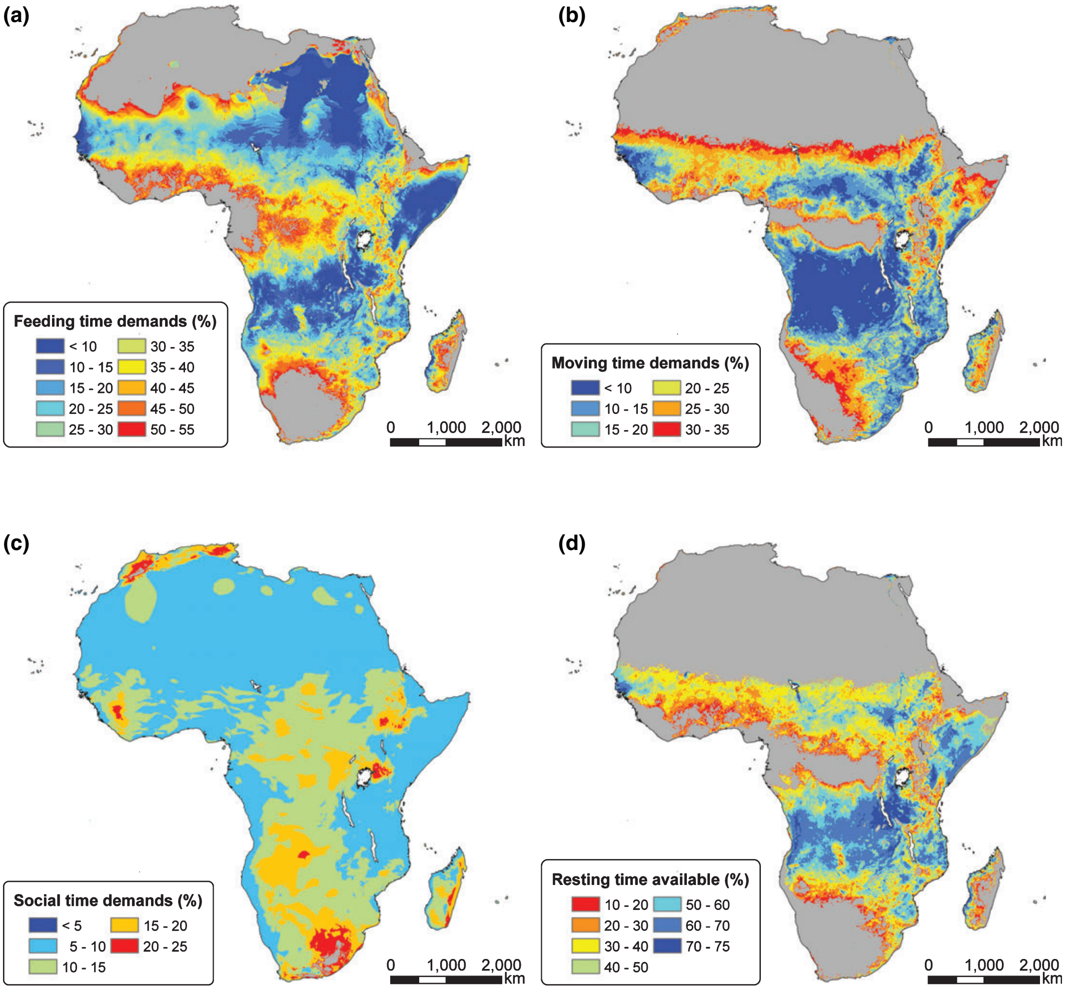

Figure 2 GIS representations of the best-fit equations for local time allocation demands on vervet monkeys (*Cercopithecus aethiops*) throughout Africa: (a) feeding time; (b) moving time; (c) social time; and (d) available resting time. Predicted values are constrained to the empirically observed range as explained in the Materials and Methods section (grey areas indicate locations where predicted time allocation demands cannot be met). This figure and all following maps are projected in the Albers Equal Area Conic coordinate system for Africa.

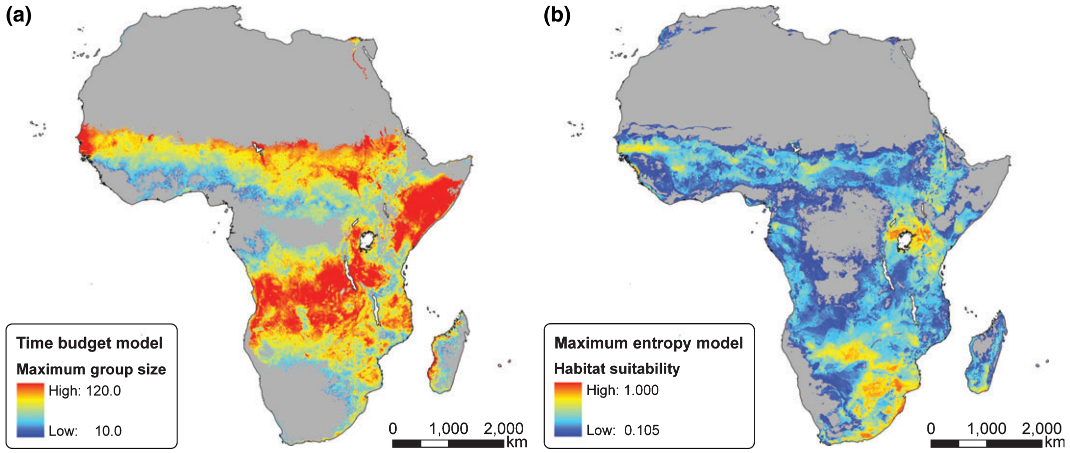

Figure 3 Ecologically maximum sustainable group size (a) and a logistic estimate of habitat suitability (b) as predicted by the time budget and maximum entropy models, respectively, for vervet monkey (*Cercopithecus aethiops*) distribution over the whole of Africa (grey indicates areas of predicted absence).

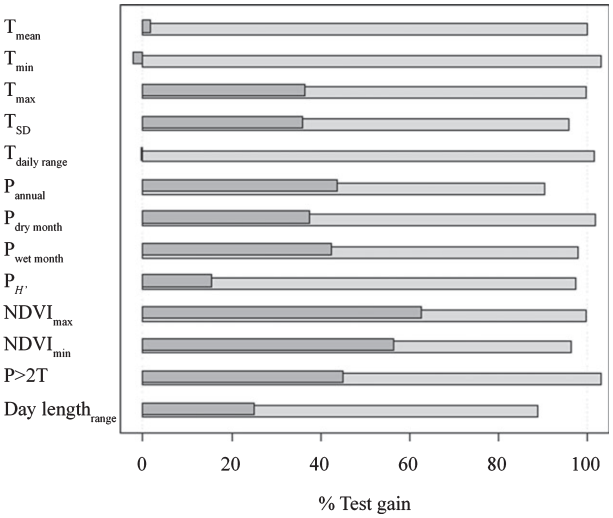

Figure 4 Results from jackknife analyses on the importance of all environmental variables in the maximum entropy model of vervet monkey (*Cercopithecus aethiops*) distribution (light bars: model performance – test gain – without variable; dark bars: model performance with variable only). T_{mean}, annual mean temperature; T_{min}, minimum temperature of the coldest month; T_{max}, maximum temperature of the warmest month; T_{SD}, temperature seasonality (standard deviation); $T_{daily\ range}$, mean diurnal temperature range; P_{annual}, annual total precipitation; $P_{dry\ month}$, total precipitation of the driest month; $P_{wet\ month}$, total precipitation of the wettest month; $P_{H'}$, rainfall seasonality (Shannon's index of evenness); $NDVI_{max}$, NDVI of the most productive month; $NDVI_{min}$, NDVI of the least productive month; P > 2T, length of growing season; Day $length_{range}$, annual range in day length.

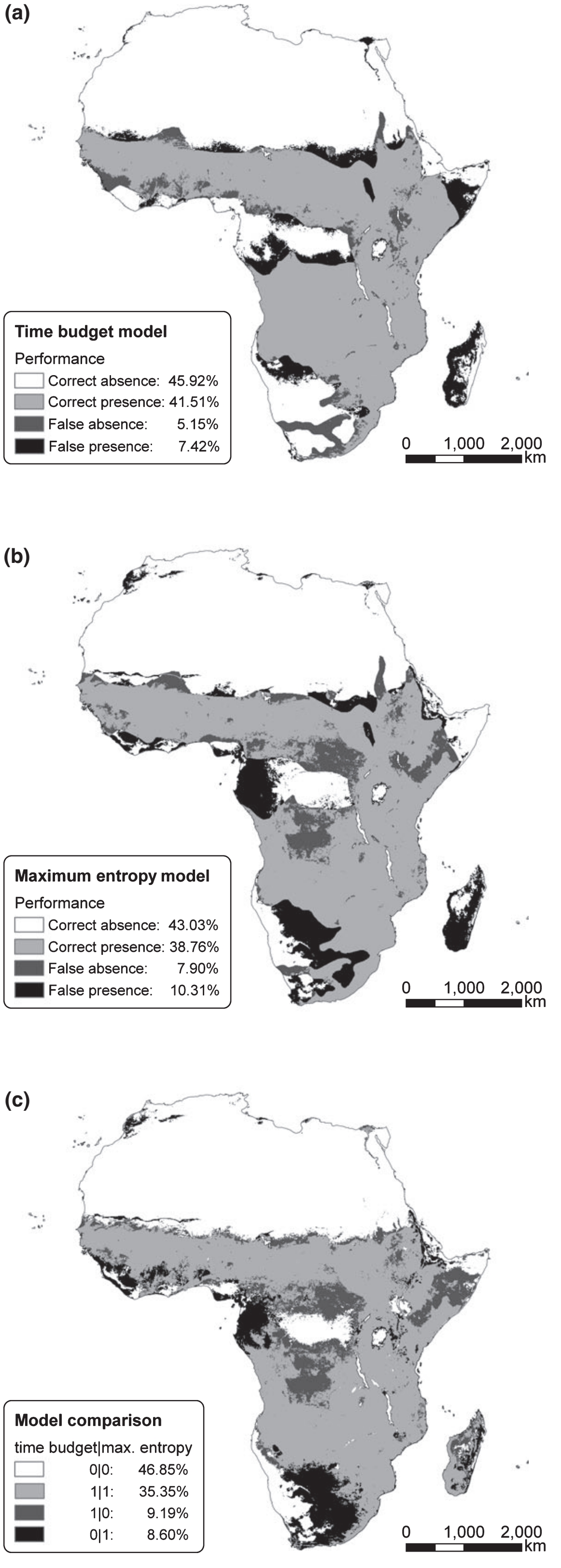

Figure 5 Geographical cross-tabulation between the binary presence–absence maps of (a) the time budget model and (b) the maximum entropy model with a reference extent of occurrence for the vervet monkey (*Cercopithecus aethiops*) in Africa. In (c) the two models are compared with each other.

accurate group counts were available (Fig. 6). In 31 populations the predicted maximum exceeded the observed maximum (86.1%), underlining again that the model performed better than random (exact binomial test: $P < 0.001$). In four of the five populations for which this was not the case, the model falsely predicted vervet monkey absence, while predicted maximum sustainable group size was smaller than the observed maximum group size in one population. Overall, predicted maximum sustainable group size (median = 69.3) was significantly larger than the corresponding observed maximum group size (median = 28.5; Wilcoxon matched-pairs test: $V = 603$, $P < 0.001$, $n = 36$). Habitat suitability as predicted by the maximum entropy model was positively related to the amount of time animals spent in social activities (Spearman's correlation: $r_s = 0.725$, $P < 0.01$, $n_{populations} = 13$).

The degree of similarity between the two species distribution models was also assessed (Fig. 5c). At 81.6% of all map pixels the respective binary presence–absence maps agreed ($\kappa_{no} = 0.631$).

DISCUSSION

Predictive modelling of species distributions is a powerful tool that features prominently in fundamental biogeographical and ecological research as well as in more applied studies of

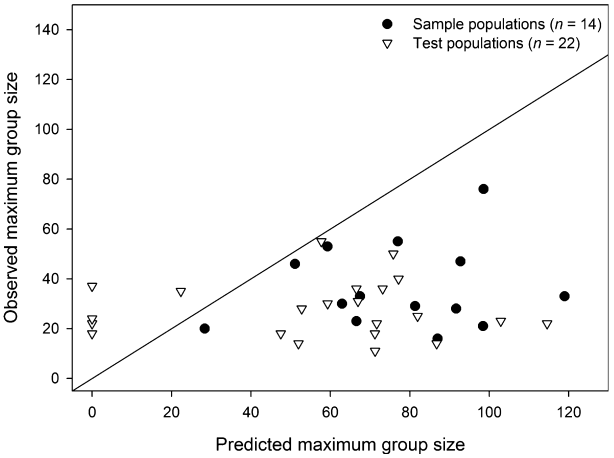

Figure 6 Comparison of the maximum ecologically tolerable group size as predicted by the time budget model and the observed maximum group sizes in the 36 populations of vervet monkey (*Cercopithecus aethiops*) throughout Africa for which accurate group counts were available. The solid line serves as a visual aid for interpretation: in the area below the line, predicted maximum group size exceeds the observed maximum group size.

conservation biology and climate change (Guisan & Zimmermann, 2000). Models typically relate simple occurrence data to environmental predictor variables and, given their ease of implementation, have found a wide range of applications. Despite the many merits of this form of correlative niche modelling, concerns have recently been expressed about the validity of the approach owing to its emphasis on methodological rather than on ecological theory (Guisan & Thuiller, 2005; Austin, 2007). Moreover, prediction in correlative modelling can often be achieved without any necessary ecological process basis (Austin, 2002). In contrast to using mere occurrence data, primatologists have often used detailed behavioural observations on time allocation and group size to predict the range of distribution of their study animals (most recently: Korstjens *et al.*, 2006; Korstjens & Dunbar, 2007; Lehmann *et al.*, 2007, 2008). This time budget approach is strongly rooted in socio-ecological theory and, here, was implemented into a GIS to allow direct comparison to a well-performing species distribution model based on presence-only data (Phillips *et al.*, 2004, 2006; Phillips & Dudík, 2008). We show that, despite lying at opposite ends of the species distribution modelling spectrum and potentially suffering from different limitations in their implementation, the time budget and maximum entropy model produce very similar results for vervet monkeys. Below we summarize the performance of both models and evaluate their respective strengths and weaknesses.

Performance of the time budget model

The time budget model explicitly aims to identify the behavioural and ecological conditions affecting vervet monkey group size and geographical distribution. Implementation into the GIS revealed that vervet monkey distribution was mainly restricted by costs associated with foraging behaviours. Both feeding and moving time demands (the latter being driven by diet composition; Table 3) precluded vervet monkeys from occurring throughout large parts of Africa (grey areas in Fig. 2). In addition, the amount of time available for resting was most adequately expressed as a negative function of feeding time and group size (Table 3). The best-fit equation for resting time thereby illustrates how time demands of one time budget component (feeding) can take precedence over those of another (resting) when the total amount of available time is limited as a result of group size (Dunbar, 1992; Janson & Goldsmith, 1995). It also underlines the notion that resting time partly consists of uncommitted time (Herbers, 1981), which serves as a reservoir from which animals can draw when time allocation demands of biologically more urgent behaviours increase (Dunbar, 1996).

The most influential ecological variable in the time budget model was annual minimum NDVI. This measure of habitat productivity was the second most significant predictor of feeding time (and thereby resting time), as well as the most significant predictor of the proportion of leaves in the diet (and thereby of moving time demands; Table 3). Vervet monkeys were predicted to be absent both from highly productive areas (the tropical rainforests of the Congo basin and West Africa) and from regions with very low levels of primary productivity (the Sahara and deserts of north-western Ethiopia and southern Africa; Fig. 3a).

Lastly, three independent tests of predictive accuracy indicated that the time budget model performed very well: vervet monkey presence was correctly predicted at 171 out of 218 independent test sites (78.4%), the degree of similarity with a reference extent of occurrence was very high (87.4%; $\kappa_{no} = 0.749$), and predicted maximum sustainable group sizes were higher than observed maximum group sizes in 31 out of 36 populations (86.1%).

Performance of the maximum entropy model

In contrast to the time budget model, the maximum entropy model does not offer any ecological mechanism to account for model predictions. Jackknife analyses of variable importance revealed that, when used in isolation, both NDVI variables yielded the highest test gain (Fig. 4). This suggests that primary productivity was the most informative predictor of vervet monkey distribution in the model. The variable that most strongly decreased model performance when omitted, on the other hand, was the annual range in day length. This variable then contained most environmental information not accounted for by any of the other predictor variables. To strictly diurnal animals, the annual range in day length reflects seasonal changes in the amount of available time within which to perform all necessary maintenance activities (Hill *et al.*, 2003, 2004). The maximum entropy algorithm, which does not necessarily achieve prediction on an ecological process basis, thereby generates statistical support for the validity of the ecological framework underlying the time budget model.

The maximum entropy model performed well and correctly predicted vervet monkey presence at 53 out of 58 independent test sites (91.4%), and the degree of similarity with a reference extent of occurrence was also high (81.8%; $\kappa_{no} = 0.636$). Moreover, model predictions on habitat suitability were strongly correlated with the amount of time animals spent in social activities. As primates have indeed been reported to spend more time in social activities in high-quality habitats (Dunbar, 1992), the maximum entropy algorithm appears to generate biologically meaningful information beyond that of simple presence–absence.

Model evaluation and comparison

Out of all species distribution models, the primatological time budget model is arguably the one most strongly rooted in ecological theory. It is also the most daring in that it makes highly falsifiable predictions on local behaviour (time allocation) and maximum sustainable group size. The time budget model thus potentially offers unparalleled insights into the socio-ecology of a species as well as the mechanisms underlying its realized distribution. However, because of its extremely high demands on the level of detail of the input data, the model is severely limited in its scope and applicability. By definition, it can only be used for animals, and, to date, sufficiently detailed behavioural information may be available for only a handful of primate species. In addition, a number of statistical reservations can be made. These include concerns about sample size (the number of populations upon which the model can be parameterized is typically small) and the cumulative build-up of errors caused by the reliance on the calculation of multiple best-fit equations to generate model predictions. In contrast, the maximum entropy model does not offer an explanation based on ecological processes, but is statistically sound and robust. Moreover, neither model explicitly incorporates variables such as dispersal, competition or other biotic interactions that may limit a species' realized distribution (Pulliam, 2000; Soberón, 2007). In this respect, however, it can be argued that, by taking a first-principles bottom-up approach based on the emergent properties of individual behaviour, the time budget model at least indirectly accounts for these confounding factors. This is true because, although the presence of a species (recorded during brief surveys) need not be at equilibrium with the local socio-ecological environment (Guisan & Thuiller, 2005), the behaviour of surviving individual animals (observed over an extended period of time) typically is (Dunbar, 1992).

Perhaps the most striking outcome of this study is that the two models generated very similar results despite their fundamentally different underlying premises and respective weaknesses. Not only were the binary presence–absence maps in strong agreement (81.6%, $\kappa_{no} = 0.631$) but both methods also identified primary productivity as the main environmental variable driving vervet monkey distribution. This is in line with previous findings on the local spatio-temporal distribution of a focal group of vervet monkeys in South Africa (Willems *et al.*, in press) and has also been reported for the population in eastern and central Eritrea (Zinner *et al.*, 2002). In addition, time was *a priori* (the time budget model) and *a posteriori* (the maximum entropy model) identified as an important resource affecting the geographical distribution of vervet monkeys. This convergence of findings from two methodologically and conceptually distinct techniques not only adds to the credibility of current results, but also relieves concerns about the validity of the two modelling approaches. Although the challenge of devising a single species distribution model that does justice to all three essential model components (the ecological, data and statistical component models) remains, the simultaneous evaluation of complementary techniques may serve as a valuable tool with which to assess the validity of model predictions. Nevertheless, where data or practical constraints permit the construction of a single model only, species distribution maps of either the time budget or maximum entropy approach can be used, as both have proved their validity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Diagnostic statistics of the time budget model.
Appendix S2 Diagnostic plots and statistics of the maximum entropy model.

BIOSKETCHES

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