Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate

Erik P. Willems, Robert A. Barton, and Russell A. Hill
Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK

Remote sensing of the environment has proved an invaluable tool to the study of animal ecology at continental to regional scales. Here, we investigated the utility of a remotely sensed index of plant productivity (the normalized difference vegetation index [NDVI]) at a much finer spatial scale to account for the range use of an omnivorous primate (the vervet monkey: *Cercopithecus aethiops*) foraging in a multipredator environment. Vervet monkey home range location suggested that the animals prefer areas with elevated productivity and reduced seasonality as indexed by simple NDVI metrics. Within the annual home range area, monthly NDVI values were linearly related to field measurements of leaf cover and quadratically associated with vervet monkey food availability. Temporal variation in parameters of local range use could subsequently be expressed in terms of local NDVI: Monthly averaged day journey length showed a second-order polynomial response, and the amount of time the monkeys spent on the ground increased with group size whereas linearly decreasing with monthly NDVI. The first finding signifies a behavioral response to food availability, whereas the latter is interpreted as an antipredatory response to changes in habitat visibility, associated with leaf cover. As a spatially explicit and temporally varying measure of habitat structure and productivity, the NDVI thus offers considerable scope for studies of animal behavioral ecology not only at broad spatiotemporal scales but also at a much finer grained level of analysis. *Key words:* geographic information system, multipredator environment, normalized difference vegetation index, remote sensing, space use, vertical substrate use. *[Behav Ecol 20:985–992 (2009)]*

One of the fundamental challenges in behavioral ecology lies in identifying the factors and processes that determine the dynamics and distribution of animals over space and time. Undeniably, the recent exponential rise in the ecological application of remotely sensed data (Kerr and Ostrovsky 2003; Turner et al. 2003) has greatly enhanced our understanding of the causal relationships linking environmental conditions to animal characteristics such as life-history traits (Rasmussen et al. 2006; Wittemyer et al. 2007), biodiversity (Hurlbert and Haskell 2003; Ruggiero and Kitzberger 2004), migration patterns (Boone et al. 2006; Ruegg et al. 2006), and species distributions (Osborne et al. 2001; Mueller et al. 2008). Out of the vast array of environmental variables that can be monitored remotely (e.g., weather conditions, topography, soil characteristics, and surface temperatures), none has proved to be of greater value to terrestrial ecologists than information on plant productivity and phenology. In particular, the normalized difference vegetation index (NDVI), a well-established correlate of photosynthetic activity and vegetation structure (Myneni et al. 1995), has frequently and successfully been employed to interpret animal characteristics in relation to vegetation properties (Pettorelli, Vik, et al. 2005). In doing so, selecting the most appropriate spatial scale of analysis has proved critical to a sound understanding of a species' ecology (Bro-Jørgensen et al. 2008).

Because one of the main advantages of remote sensing lies in the fact that it greatly facilitates the monitoring of large areas at frequent time intervals, the vast majority of studies utilizing remotely sensed information have focused on a continental-to-regional scale. In animal ecology, this has inadvertently led to a bias in the application of remotely sensed data toward wide-ranging taxa (birds: Evans et al. 2006; carnivores: Herfindal et al. 2005; ungulates: Ito et al. 2006). Consequently, the value of remote sensing to the finer grained socioecological dynamics of less widely dispersing species remains largely unexplored. What is more, its potential to explain temporal variation in range use at such small scales has never explicitly been assessed. The primary aim of this study, then, is to investigate the utility of the NDVI as a spatially explicit and temporally varying measure of habitat productivity to account for regional and local aspects of animal space use. This is examined using detailed behavioral and ecological observations on a group of wild vervet monkeys (*Cercopithecus aethiops*).

A recent survey on the distribution of vervet monkeys in central and eastern Eritrea reported that estimated home ranges had significantly higher average NDVI values than the entire area of survey (Zinner et al. 2002). This finding not only strongly suggests that local NDVI values contain valuable environmental information but also suggests that this information can be used to investigate the selection of home range location in vervet monkeys. Here, we build on this finding by examining an empirically established home range of a focal group and evaluating temporal aspects of range use within this home range in relation to a time series of local NDVI values. More specifically, the utility of the NDVI on this localized level of analysis is assessed in 3 distinct ways. First, annual average productivity and seasonality as expressed by simple NDVI metrics are calculated over the home range area and

compared with those of its immediate surroundings and broader ecoregion. We then further refine the scale of analysis by, second, assessing NDVI values over the home range for their ecological information content by comparisons to accurate field measurements on habitat productivity and plant phenology throughout the home range. Third, temporal variation in 3 monthly parameters of local range use (size of core area, average day journey length, and average level of terrestriality) is linked to a NDVI time series constructed over the home range. Overall, we provide convincing support for the value of the NDVI as a tool for the study of local and short-term dynamics of animal distribution. In addition, we propose 2 ecologically distinct interpretations of the relationship between local NDVI values and range use that are of considerable importance to the understanding of vervet monkey socioecology in particular and animal behavioral ecology in general.

METHODS

Study species and field site

The vervet monkey (*C. aethiops* subspp.) is an opportunistic omnivore with an overwhelmingly frugivorous diet and highly flexible behavioral repertoire. Although generally absent from deserts and tropical rainforests, vervet monkeys occur in a wide range of habitats throughout sub-Saharan Africa (Willems et al. forthcoming). Animals are active during daylight hours and maintain a semiterrestrial, semiarboreal lifestyle that, in combination with a small body size (males: 4–8 kg, females: 3–5 kg), renders them susceptible to predation by a wide range of predators (Willems and Hill 2009). Multimale and multifemale groups, typically of around 20 individuals, occupy stable home ranges that may overlap to varying degrees. In comparison to taxa used in previous studies relating animal range use to remotely sensed primary productivity, vervet monkeys range over very small areas (home range size [mean ± standard deviation {SD}]: $0.80 ± 0.70$ km^2, day journey length [mean ± SD]: $1.24 ± 0.57$ km, $n_{populations} = 17$; Willems 2007). This greatly facilitates the monitoring of key ecological variables in the field throughout an entire home range. The animals themselves, moreover, readily habituate to the presence of human observers and thereby allow the collection of highly detailed data on range use and associated behaviors. Vervet monkeys thus make an excellent species to investigate the usefulness of remote sensing on a small absolute scale, while considering ecological as well as behavioral factors (cf. Bro-Jørgensen et al. 2008).

Fieldwork was conducted at the Lajuma Research Centre in the western part of the Soutpansberg Mountain range, South Africa ($23°02'$ S, $29°26'$ E). Lajuma is situated in a mountainous environment (on-site altitudinal range: 1150–1750 m) with a complex mosaic of diverse habitat types that are classified under the unique Soutpansberg mist-belt forest group (von Maltitz 2003). Local climatic conditions are mesothermal with cool dry winters (April–September) and warm wet summers (October–March). On-site annual mean temperature averages at 17.1 °C, and average total annual rainfall is 724 mm (Willems 2007).

Behavioral sampling

A single group of vervet monkeys was selected for behavioral monitoring. At the onset of data collection, all animals within the group ($n_{mean} = 17.8$, $n_{range} = 13–24$) were individually recognized and allowed a human observer (E.P.W.) to approach within 5 m without showing any notable behavioral response. Information on range use was collected on handheld computers (Palmtop Zire 21) equipped with behavioral

data collection software (Pendragon Software Corporation 2003) and on a handheld GPS device (Garmin GPS 72). The group was followed on foot for 7 successful days each month, scheduled to achieve an even distribution over the month. Successful days were defined as days on which the animals could be observed traveling from morning sleeping tree to evening sleeping tree without losing audiovisual contact for a continuous period exceeding 60 min. This yielded a total of 84 follow days over the entire observation period (May 2005–April 2006). Geographic coordinates on the center of mass of the group (Altmann and Altmann 1970) were obtained at the onset and cessation of all activity at dawn and dusk as well as at fixed 30-min intervals throughout the day. Group spread was typically well more than 50 m, thereby relieving possible concerns about the accuracy of telemetric measurements in a mountainous environment (mean ± SD = $6.9 ± 2.3$ m, $n = 2208$). During the 5 min immediately preceding each 30-min interval, the proportion of animals on the ground was scored by instantaneous group scan sampling (Martin and Bateson 1993).

Environmental monitoring in the field

Two aspects of home range productivity were extensively monitored in the field: primary productivity and food availability. Information on the presence, abundance, and developmental stage of leaves (primary productivity) and flowers, fruits, and seeds (food availability) was recorded from individually marked trees ($n_{species} = 9$, $n_{trees\ per\ species} = 10$) during monthly transects. Trees were selected throughout the home range to obtain a proportional representation of all habitat types to most faithfully capture local phenology. Reproductive structures of the selected species accounted for more than 40% of the study group's total feeding time over the observation period (median$_{monthly}$ = 47.7%, interquartile range = 29.9–51.5%). Combined with data on habitat-specific species density obtained from quadrat sampling (75 plots of 100 m^2 each), monthly estimates on leaf cover and the number of food items within the entire home range were calculated. Data on food availability required log transformation prior to analysis to achieve a normal distribution.

Remote sensing of the environment

Remotely sensed information on primary productivity and plant phenology was collated from NDVI data collected by the moderate resolution imaging spectrometer (MODIS) on board of NASA's TERRA satellite (Huete et al. 2002). The NDVI is a spectral index calculated from earth surface reflectance patterns in the red and near-infrared regions of the electromagnetic spectrum and enhances the detection of plant properties (Tucker 1979). A dimensionless index, the NDVI, can take values between -1 and 1, where low values correspond to an absence of vegetation and higher, positive values signify a photosynthetically more active substrate. Data were retrieved from the Earth Resources Observation System Web site (http://eros.usgs.gov/products/satellite.html), and monthly maximum value composites (Holben 1986) were created from the MOD 13Q data set (local effective resolution after rectification—i.e., "pixel size"—232 m) over 3 spatial extents: 1) the entire Soutpansberg Mountain range (ca. 3300 km^2); 2) an area incorporating the Lajuma Research Centre, referred to as Greater Lajuma (64 km^2); and 3) the home range area of the study group (1.14 km^2; see below). An exceptionally high monthly maximum value composite over the home range during January 2006 was discarded after examinations of its associated quality assessment data sets (MODIS VI QA SDS) and substituted by the mean of the

maximum value composites over December 2005 and February 2006. This correction did not affect the outcome of any ensuing analysis. Seasonality in productivity (plant phenology) was expressed as the coefficient of variation (%) of monthly NDVI pixel values, averaged over each of the 3 areas of interest. NDVI data were imported and prepared for analysis using IDRISI Andes (Eastmann 2006).

Geographic information system model

All spatial information was imported into a geographic information system (GIS; ArcGIS Desktop 9.0 [ESRI 2004]). Within the GIS, an orthorectified Quickbird satellite image (acquisition date: 5 October 2004, local effective resolution: 0.56 m) served as a base map, whereas altitudinal information was incorporated by a digital elevation model (DEM) of the study area. The DEM was constructed from 20-m contour lines, spot heights, and trigonometric beacons digitized from the South African national topography map series (national grid cell 2329AB, scale 1:50 000). Data were projected in the Universal Transverse Mercator coordinate system (datum: WGS 1984, zone: 35 S).

Parameters of range use and statistical analysis

Based on behavioral field observations, 3 range use parameters were calculated within the annual home range: monthly core area, monthly averaged day journey length, and monthly averaged level of terrestriality.

Monthly core areas (delineated by 50% volume isopleths) and the annual home range (delineated by a 99% volume isopleth) were computed by kernel density estimation in the Home Range Tools extension for ArcGIS (Rodgers et al. 2007). Kernel density estimation (Silverman 1986) is currently one of the more robust and most widely applied techniques in spatial ecology for quantifying animal range use (de Solla et al. 1999; Börger et al. 2006). Here, a fixed Gaussian kernel, relying on least squares cross-validation to parameterize the kernel's bandwidth, was chosen (Gitzen et al. 2006). To ensure that outcomes of this procedure were proportional to the amount of time the animals spent at each location, only GPS coordinates collected at a constant time interval ($\Delta t = 30$ min, $n = 2040$) were entered into the kernel analyses (Anderson 1982; Seaman and Powell 1996). The respective sizes of monthly core areas and the total home range (1.14 km^2) were computed as 3D true surface areas derived from the DEM of the study area (Figure 1).

Day journey lengths were calculated within the GIS by summing daily straight-line distances between sequential GPS coordinates ($n_{\text{daily mean}} \pm \text{SD} = 26.3 \pm 1.9$). Analogous to the computation of true surface areas, altitudinal information from the DEM was incorporated into the estimates of 3D day journey lengths (Figure 1).

The final range use parameter considered here was the proportion of time that animals spent on the ground. Data were available for 79 out of the 84 successful follow days. As this information was obtained through animal counts stemming from instantaneous group scan samples ($n = 8073$), an arcsine ($\sqrt{x}$) transformation was applied to permit parametric analysis.

Statistical analyses were conducted in R 2.7.0 (R Development Core Team 2008), SPSS 15.0 (SPSS Inc 2006), and SAM 3.0 (Rangel et al. 2006).

RESULTS

NDVI over annual home range and broader environment

Monthly primary productivity over the home range, its immediate surroundings (Greater Lajuma), and broader ecoregion
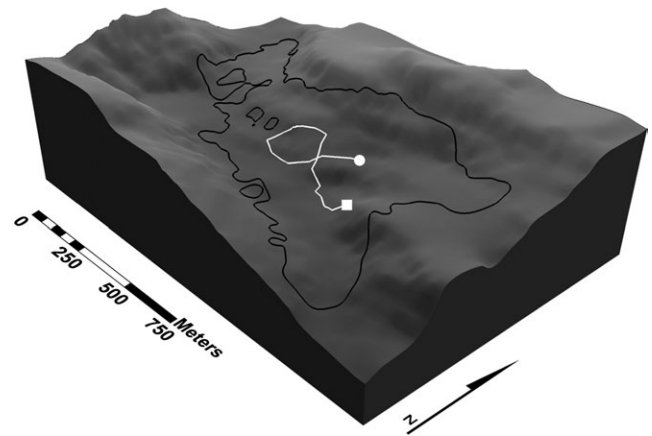

Figure 1
3D representation of the DEM of the study site. The black-outlined polygon demarcates the annual home range of the study group (1.14 km^2), whereas the white line depicts an exemplar day journey trajectory (circle and square indicates the location of morning and evening sleeping trees, respectively).

(the Soutpansberg; Figure 2a) were analyzed using a linear mixed-effects model (Pinheiro and Bates 2000). This comparison was biologically meaningful because the home range was highly representative of the Soutpansberg Mountain range in terms of its vegetation structure (all terrestrial biomes identified within the Soutpansberg region—forest, thicket, savanna, and grassland–were present in the home range area). Contrast coefficients within the model were defined to obtain pairwise comparisons between the 3 areas and relied on Bonferroni-corrected P values to assess significance. Moreover, to account for the potentially confounding effect of spatial autocorrelation (Legendre 1993), model parameters and associated confidence intervals were estimated by a spatial bootstrap on model residuals ($n_{\text{simulations}} = 50$; Efron and Tibshirani 1993; Pettorelli, Mysterud, et al. 2005; Bro-Jørgensen et al. 2008). Pixels within the Greater Lajuma and the Soutpansberg regions that, by their very nature, precluded vervet monkey presence (e.g., lakes) were excluded from the analyses.

Both the model and spatial bootstrap indicated that NDVI values over the home range were significantly higher than over either Greater Lajuma ($t = 18.40$, $P < 0.001$) or the Soutpansberg ($t = 11.25$, $P < 0.001$). In addition, NDVI values over the Soutpansberg were significantly higher than those over Greater Lajuma ($t = 54.3$, $P < 0.001$). The home range area of the study group thus exhibited consistently higher monthly NDVI values than its broader ecoregion (the Soutpansberg), despite being situated in a section (Greater Lajuma) with consistently lower monthly productivity levels than those of the broader ecoregion.

Seasonality in productivity over the 3 areas (Figure 2b) was analyzed by a linear model in which contrasts were set to generate Bonferroni-corrected pairwise comparisons. Again, spatial autocorrelation was controlled for by spatially bootstrapping model residuals. Seasonality was less pronounced over the home range than over either Greater Lajuma ($t = 2.52$, $P < 0.05$) or the Soutpansberg ($t = 3.67$, $P < 0.001$). Seasonality over Greater Lajuma, moreover, was less prominent than over the Soutpansberg region ($t = 8.34$, $P < 0.001$).

Local NDVI and field measurements of habitat productivity

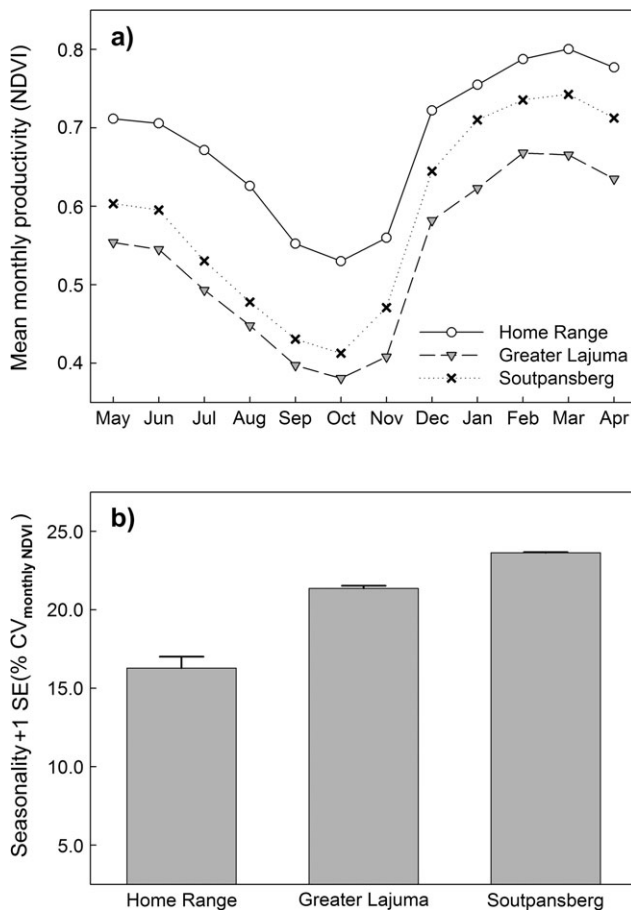To gage and validate the ecological information content of NDVI values over the home range of the study group, monthly

Figure 2
Mean monthly primary productivity (a) and annual seasonality (b) as expressed by simple NDVI metrics over the 3 areas under investigation (error bars in [a] are omitted for clarity).

Table 1

Summary of correlation analyses linking remotely sensed productivity (NDVI) and 3 parameters of local range use to different aspects of habitat productivity as measured in the field and by satellite

	Leaf cover	Log (food)	NDVI
NDVI			
$r_{pearson}$	0.923	−0.213	—
P	<0.001	0.845[a]	—
Core area			
$r_{semipartial}$	−0.233	0.386	−0.100
P	0.514	0.235	0.767
Day journey length			
$r_{semipartial}$	−0.379	−0.849	−0.619
P	0.269	<0.001	<0.050
Terrestriality			
$r_{semipartial}$	−0.740	−0.218	−0.746
P	<0.001	0.416	<0.001

Associations between range use and productivity were controlled for the confounding effect of variation in group size on range use. $n = 12$.
[a] No significant linear association detected but see Figure 3.

NDVI values, whereas the level of terrestriality showed a negative association with leaf cover and NDVI.

Range use as a function of local NDVI

Combining results from the preceding analyses, best minimal adequate models (selected on the basis of the corrected Akaike information criterion [AICc]; Burnham and Anderson 2002) were determined for monthly averaged day journey length and level of terrestriality. The model selection procedure considered all biologically meaningful combinations of 4 predictor variables: a linear NDVI term, a second-order polynomial of NDVI values, group size, and the complementary range use parameter (day journey length and terrestriality were interrelated; Supplementary Appendix 1). Models with the lowest AICc values are presented in Table 2. On the basis of current observations, monthly averaged day journey length was best expressed by a second-order polynomial function of monthly NDVI (which relates to food availability; Figure 3), whereas the level of terrestriality was best explained by a positive
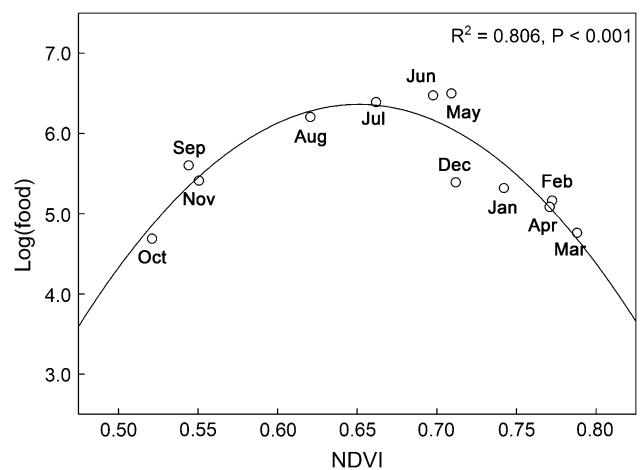
values were assessed for their association with traditional proxies of habitat productivity as measured in the field. Monthly NDVI values were strongly and linearly related to field estimates of leaf cover but not to food availability (Table 1). Inspections of the scatter plot, however, revealed a significant second-order polynomial relationship, denoting how peaks in food availability coincided with months of intermediate NDVI values (Figure 3).

Range use, field measurements of habitat productivity, and local NDVI

Two out of 3 parameters of local range use showed significant cubic trends over the observation period (planned polynomial contrasts; day journey length: $F_{1,72} = 7.71$, $P < 0.01$; terrestriality: $F_{1,67} = 16.85$, $P < 0.001$; Figure 4), exhibiting a similar but inverted pattern as local NDVI values (Figure 2a). To assess whether temporal variation in all 3 range use parameters was related to aspects of habitat productivity, first-order semipartial correlations were conducted to control for the confounding effect of variation in group size over the study period on range use (Supplementary Appendix 1).

The size of monthly core areas did not relate to either field measure of habitat productivity or monthly NDVI values over the home range (Table 1). Day journey length, on the other hand, was negatively related to food availability and monthly

Figure 3
Scatter plot with fitted second-order polynomial curve relating monthly NDVI values over the home range to log-transformed field estimates of local food availability.
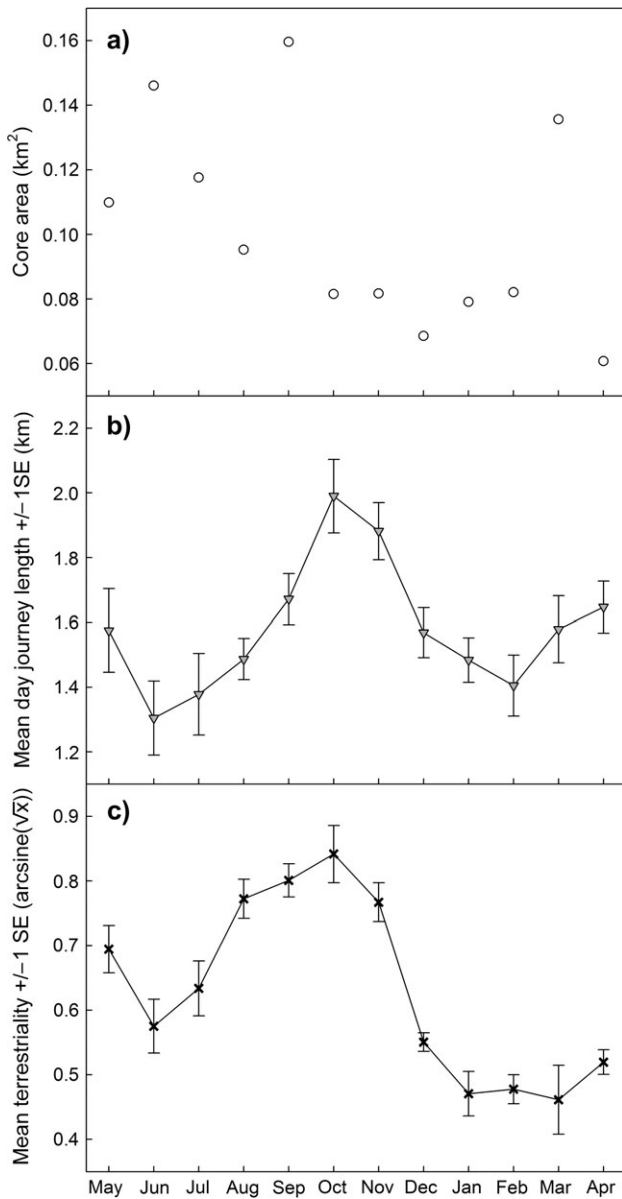
Figure 4
Temporal profiles of 3 parameters of local range use: (a) size of monthly core areas, (b) monthly averaged day journey length, and (c) monthly averaged level of terrestriality (transformed to allow parametric analysis). Lines indicate cubic trends within monthly values of mean day journey length and level of terrestriality.

Table 2

Parameter estimates and key statistics of the AICc-selected best minimal adequate models for monthly averaged day journey length and level of terrestriality

	B	SE_B	β	$t_{(\beta = 0)}$	$P_{(\beta = 0)}$	F_{model}	SE_{model}	R^2_{adj}
DJL								
Intercept	9.82	2.25		4.36	<0.001	11.65	0.12	0.659
NDVI^2	17.59	5.35	10.92	3.29	0.009			
NDVI	−24.30	7.00	−11.53	−3.47	0.007			
Terre								
Intercept	1.22	0.19		6.53	<0.001	52.89	4.11	0.904
Group size	0.02	0.01	0.22	2.09	0.066			
NDVI	−1.22	0.15	−0.84	−7.99	<0.001			

$n = 12$; SE, standard error; DJL, day journey length: $P < 0.005$; Terre, level of terrestriality: $P < 0.001$.

(continental to regional) areas. In this study, its power to account for animal space use at a much smaller absolute scale was investigated by looking at regional and local aspects of range use by a group of wild vervet monkeys.

Home range selection at a regional scale

Habitat productivity as assessed by monthly NDVI values was both higher and less seasonal over the home range area of a focal group of vervet monkeys than over its immediate surroundings and broader ecoregion. Two previous studies on primate distribution reported that hypothetical circular home ranges of baboons (*Papio hamadryas* subspp.; 28.3 km^2) and vervet monkeys (0.79 km^2) in Eritrea had higher NDVI values than the complete area of survey (22 000 km^2; Zinner et al. 2001, 2002). Similar results have also been reported for empirically established home ranges of other animal taxa, albeit at much larger scales (e.g., Ryan et al. 2006). Here, for the first time, the NDVI was employed to investigate the selection of the location of an empirically established primate home range. At this scale, both overall habitat productivity and seasonality were found to be of importance. This interpretation is particularly supported, given that 1) pixels within the Greater Lajuma and the Soutpansberg regions that precluded vervet monkey presence were excluded from the analyses and 2) monthly NDVI values were not only consistently higher but also less variable over the home range area. Crucially, the latter finding cannot be explained by differences in vegetation density or structure between the 3 areas (which, alternatively, could account for the higher monthly values over the home range) but instead is readily understood in terms of less pronounced seasonality in productivity.

Temporal variation in local range use and interpretations of local NDVI

Further reducing the granularity of analysis, temporal variation in 3 parameters of local range use was investigated within the home range of the study group.

The size of monthly core areas was neither related to monthly NDVI values over the annual home range nor to field estimates on 2 aspects of habitat productivity. Interpreted in the light of the findings at the regional and annual level, it is likely that at the local and monthly level the monkeys selected the location of core areas on the basis of productivity as well. This would enable them to mitigate the effects of seasonal variation in productivity without having to adjust the size of monthly core areas (the fact that monthly core areas did vary in size—Figure 4a—may indicate that other socioecological
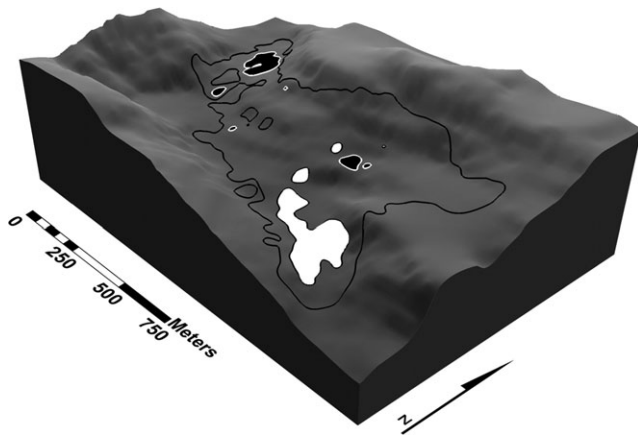
function of group size and a negative linear NDVI term (related to leaf cover; Table 1).

DISCUSSION

The last couple of decades have seen an exponential rise in the ecological application of remotely sensed data. Remote sensing has opened up a new realm of research perspectives and continues to prove an invaluable data source for biologists from varying fields (Kerr and Ostrovsky 2003; Turner et al. 2003). In particular, the NDVI, an index of vegetation structure and vigor, has facilitated unprecedented insights into the functioning of terrestrial ecosystems (Pettorelli, Vik, et al. 2005). Within behavioral ecology, the NDVI has typically been used to interpret animal dynamics and distributions over large

Figure 5
Locations of 2 exemplar monthly core areas (white-filled polygon, January 2006; black-filled polygon, April 2006) within the annual home range of the study group, suggesting that the location of monthly ranging areas may vary spatially.

factors were at play). Qualitative evidence for this comes from examinations of range use maps that reveal clear spatial shifts in the locality of monthly centers of activity (Figure 5). Unfortunately, a quantitative analysis of this hypothesized spatial selection of core areas within the home range could not be conducted (but see Supplementary Appendix 2 for an alternative approach) as individual polygons constituting monthly core areas were often smaller than NDVI pixel size (0.054 km^2). At much coarser spatiotemporal scales though, studies on ungulates do provide compelling evidence that animals indeed select the location of seasonal ranges in response to spatially varying levels of productivity as indexed by the NDVI (Boone et al. 2006; Ito et al. 2006; van Bommel et al. 2006; Mueller et al. 2008). With the current spatial resolution of freely available satellite imagery then, spatially explicit studies on widely dispersing taxa can achieve a relatively finer grain of analysis, despite being coarser at the absolute level. The NDVI, however, is readily computed from other hyperspatial satellite sensors, and these offer imagery with spatial resolutions of up to less than 1 m at similar sampling intervals (revisit times of 1–5 days; e.g., IKONOS, OrbView, Quickbird). These sensors therefore hold enormous promise for future studies of space use by locally ranging animals, such as the one presented here.

Monthly averaged day journey length was strongly and negatively related to NDVI values and field estimates of food availability, suggesting that the animals had to cover a greater distance during months of low productivity and food availability to meet metabolic demands. This is a commonly observed pattern within the primate order (e.g., Barton et al. 1992) but has never been established using remotely sensed information. Using NDVI data at a much coarser spatiotemporal resolution, a similar result was found in African buffalo (*Syncerus caffer*) as a focal herd traveled further over 10-day blocks during the dry season than during the wet season (Ryan et al. 2006). This was taken to imply that the herd either moved further in search of food or that more time had to be spent moving and grazing due to impoverished food quality. Both explanations may account for the relationship reported here, but a more in-depth investigation revealed a second-order polynomial relationship between local NDVI values and food availability for the nonherbivorous vervet monkeys. This nonlinear association reflects the reproductive strategies of the main food species on-site that produce reproductive struc-

tures (flowers, fruits, and seeds) during months of leaf flushing and abscission, reminiscent of a phenological spring and autumn at more temperate latitudes. In the current study system then, intermediate NDVI values correspond with peaks in food availability, whereas food is least abundant during months of high and low levels of leaf cover. It would be interesting to examine whether this represents a more general association between monthly food availability for frugivorous animals and overall habitat productivity or whether it is merely a fortunate feature of the local phenology at the study site. Either way, selection of a best minimal adequate model subsequently confirmed that the monkeys adjusted travel distance in accordance to local food availability rather than primary productivity per se: Day journey length was best expressed by a second-order polynomial function of local NDVI values. Interestingly, distribution patterns of the strictly herbivorous Mongolian gazelle (*Procapra gutturosa*) were also most adequately modeled by a second-order polynomial function of NDVI values (Mueller et al. 2008). This relationship, however, arose from a trade-off between low ingestion rates (associated with low NDVI values) and low digestibility of mature forage (associated with high NDVI values), whereas the more frugivorous vervet monkeys responded to local food availability only.

The monthly level of terrestriality was negatively related to local NDVI values and field estimates of leaf cover (which were strongly and linearly related). This result could indirectly have arisen due to food being most abundant on the forest floor in the form of drought-persistent seeds and pods during the least productive months. For a nonfolivorous species foraging in a multipredator environment (Willems and Hill 2009), however, arguably, the most relevant environmental parameter directly associated with the NDVI, and leaf cover is habitat visibility. In months with high levels of leaf cover, visibility is low, and this increases the risk of attack by terrestrial ambush predators (e.g., leopard, *Panthera pardus*; Cowlishaw 1997) whereas decreasing the risk of detection by aerial predators (e.g., crowned eagle, *Stephanoaetus coronatus*). Therefore, to the monkeys, an increase in NDVI values over the home range may represent an increase in the risk of terrestriality and a decrease in the risk of arboreality. The study group adaptively responded to this by adjusting substrate use in the observed manner, minimizing the risk of predation. Although changes in vertical substrate use and terrestriality in primates have previously been related to perceived predation risk (McGraw and Bshary 2002; Campbell et al. 2005), this has not been done before using remotely sensed data. Further substantiating the perceived predation risk hypothesis, the AICc-selected best minimal adequate model expressed terrestriality as a positive function of group size and a negative function of monthly NDVI. This underscores previous findings that larger primate groups benefit from increased protection against terrestrial predators but not against aerial predators (Shultz et al. 2004) as well as that habitat visibility affects perceived predation risk (Cowlishaw 1997; Hill and Weingrill 2006).

Conclusion

Although the NDVI has frequently been applied to understand how vegetation characteristics affect animal diversity, life-history traits, population dynamics, and movement patterns (Pettorelli, Vik, et al. 2005), previous investigations have almost exclusively been conducted at broad spatial scales. Here, we have demonstrated that the NDVI, complemented with detailed field measurements on crucial aspects of habitat productivity from the perspective of the study species, can also be used to successfully account for animal distribution and space use at much smaller scales. Regional

selection of home range location and temporal variation in local range use by a focal group of vervet monkeys were both related to the NDVI. Moreover, monthly NDVI values over the home range were associated with key characteristics of the ecological environment of the study group. Leaf cover (and thereby habitat visibility and, ultimately, predator guild-specific predation risk) was a linear function of local NDVI values, whereas food availability could be expressed as a second-order polynomial of local NDVI. Based on these findings, and given the ever-improving spatial resolution of satellite-mounted sensors, remotely sensed indices of habitat productivity and vegetation structure will continue to offer enormous potential to the study of animal ecology across a broad range of species and spatial scales for decades to come. The successful application of this wealth of information from space-borne data collection platforms, however, will critically hinge on complementary data from the field to warrant sound ecological interpretation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/.

FUNDING

REFERENCES

Altmann SA, Altmann J. 1970. Baboon ecology. Chicago: Chicago University Press.
Anderson DJ. 1982. The home range: a new nonparametric-estimation technique. Ecology. 63:103–112.
Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ. 1992. Habitat use and resource availability in baboons. Anim Behav. 43:831–844.
Boone RB, Thirgood SJ, Hopcraft JGC. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology. 87:1987–1994.
Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol. 75:1393–1405.
Bro-Jørgensen J, Brown ME, Pettorelli N. 2008. Using the satellite-derived normalized difference vegetation index (NDVI) to explain ranging patterns in a lek-breeding antelope: the importance of scale. Oecologia. 158:177–182.
Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. New York: Springer.
Campbell CJ, Aureli F, Chapman CA, Ramos-Fernandez G, Matthews K, Russo SE, Suarez S, Vick L. 2005. Terrestrial behavior of Ateles spp. Int J Primatol. 26:1039–1051.
Cowlishaw G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Anim Behav. 53:667–686.
de Solla SR, Bonduriansky R, Brooks RJ. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. J Anim Ecol. 68:221–234.
Eastmann JR. 2006. IDRISI Andes: guide to GIS and image processing. Worcester (MA): Clark Labs, Clark University.
Efron B, Tibshirani RJ. 1993. An introduction to the bootstrap. New York: Chapman & Hall.

ESRI. 2004. ArcGis 9.0. Redlands (CA): Environmental Systems Research Institute, Inc.
Evans KL, James NA, Gaston KJ. 2006. Abundance, species richness and energy availability in the North American avifauna. Glob Ecol Biogeogr. 15:372–385.
Gitzen RA, Millspaugh JJ, Kernohan BJ. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. J Wildl Manage. 70:1334–1344.
Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R. 2005. Prey density, environmental productivity and home-rancre size in the Eurasian lynx (Lynx lynx). J Zool. 265:63–71.
Hill RA, Weingrill T. 2006. Predation risk and habitat use in chacma baboons (Papio hamadryas ursinus). In: Gursky S, Nekaris KAI, editors. Primates and their predators. New York: Kluwer Academic Publishers. p. 339–354.
Holben BN. 1986. Characteristics of maximum-value composite images from temporal AVHRR data. Int J Remote Sens. 7:1417–1434.
Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens Environ. 83:195–213.
Hurlbert AH, Haskell JP. 2003. The effect of energy and seasonality on avian species richness and community composition. Am Nat. 161:83–97.
Ito TY, Miura N, Lhagvasuren B, Enkhbileg D, Takatsuki S, Tsunekawa A, Jiang Z. 2006. Satellite tracking of Mongolian gazelles (Procapra gutturosa) and habitat shifts in their seasonal ranges. J Zool. 269:291–298.
Kerr JT, Ostrovsky M. 2003. From space to species: ecological applications for remote sensing. Trends Ecol Evol. 18:299–305.
Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm. Ecology. 74:1659–1673.
Martin P, Bateson P. 1993. Measuring behaviour: an introductory guide. 2nd ed. Cambridge (UK): Cambridge University Press.
McGraw WS, Bshary R. 2002. Association of terrestrial mangabeys (Cercocebus atys) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. Int J Primatol. 23:311–325.
Mueller T, Olson KA, Fuller TK, Schaller GB, Murray MG, Leimgruber P. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. J Appl Ecol. 45:649–658.
Myneni RB, Hall FG, Sellers PJ, Marshak AL. 1995. The interpretation of spectral vegetation indexes. IEEE Trans Geosci Remote Sens. 33:481–486.
Osborne PE, Alonso JC, Bryant RG. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. J Appl Ecol. 38:458–471.
Pendragon Software Corporation. 2003. Pendragon Forms. 4.0. Libertyville, IL: Pendragon Software.
Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proc R Soc Lond Ser B Biol Sci. 272:2357–2364.
Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol Evol. 20:503–510.
Pinheiro JC, Bates DM. 2000. Mixed-effects models in S and S-Plus. New York: Springer-Verlag.
R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
Rangel T, Diniz-Filho JAF, Bini LM. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. Glob Ecol Biogeogr. 15:321–327.
Rasmussen HB, Wittemyer G, Douglas-Hamilton I. 2006. Predicting time-specific changes in demographic processes using remote-sensing data. J Appl Ecol. 43:366–376.
Rodgers AR, Carr AP, Beyer HL, Kie JG. 2007. HRT: home range tools for ArcGIS. 1.1 ed. Ontario (Canada): Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research.
Ruegg KC, Hijmans RJ, Moritz C. 2006. Climate change and the origin of migratory pathways in the Swainson's thrush, Catharus ustulatus. J Biogeogr. 33:1172–1182.
Ruggiero A, Kitzberger T. 2004. Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. Ecography. 27:401–416.

Ryan SJ, Knechtel CU, Getz WM. 2006. Range and habitat selection of African buffalo in South Africa. J Wildl Manage. 70:764–776.

Seaman DE, Powell RA. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology. 77:2075–2085.

Shultz S, Noë R, McGraw WS, Dunbar RIM. 2004. A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. Proc R Soc Lond Ser B Biol Sci. 271:725–732.

Silverman BW. 1986. Density estimation for statistics and data analysis. London: Chapman and Hall.

SPSS Inc. 2006. SPSS for Windows 15.0. Chicago: SPSS.

Tucker CJ. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sens Environ. 8:127–150.

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M. 2003. Remote sensing for biodiversity science and conservation. Trends Ecol Evol. 18:306–314.

van Bommel FPJ, Heitkonig IMA, Epema GF, Ringrose S, Bonyongo C, Veenendaal EM. 2006. Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana. J Trop Ecol. 22:101–110.

von Maltitz G. 2003. Classification system for South African indigenous forests. Pretoria (South Africa): Environmentek CSIR.

Willems EP. 2007. From space to species: integrating remotely sensed information on primary productivity into investigations and systems models of vervet monkey (*Cercopithecus aethiops*) socio-ecology [PhD thesis]. [Durham (UK)]: Durham University.

Willems EP, Barton RA, Hill RA. Forthcoming. A critical assessment of two species distribution models: a case study of the vervet monkey (*Cercopithecus aethiops*). J Biogeogr.

Willems EP, Hill RA. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. Ecology. 90:546–555.

Wittemyer G, Rasmussen HB, Douglas-Hamilton I. 2007. Breeding phenology in relation to NDVI variability in free-ranging African elephant. Ecography. 30:42–50.

Zinner D, Pelaez F, Torkler F. 2001. Distribution and habitat associations of baboons (*Papio hamadryas*) in Central Eritrea. Int J Primatol. 22:397–413.

Zinner D, Pelaez F, Torkler F. 2002. Distribution and habitat of grivet monkeys (*Cercopithecus aethiops aethiops*) in eastern and central Eritrea. Afr J Ecol. 40:151–158.