



Original Article

# Feeding habitat quality and behavioral trade-offs in chimpanzees: a case for species distribution models

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The distribution and abundance of food resources are among the most important factors that influence animal behavioral strategies. Yet, spatial variation in feeding habitat quality is often difficult to assess with traditional methods that rely on extrapolation from plot survey data or remote sensing. Here, we show that maximum entropy species distribution modeling can be used to successfully predict small-scale variation in the distribution of 24 important plant food species for chimpanzees at Gombe National Park, Tanzania. We combined model predictions with behavioral observations to quantify feeding habitat quality as the cumulative dietary proportion of the species predicted to occur in a given location. This measure exhibited considerable spatial heterogeneity with elevation and latitude, both within and across main habitat types. We used model results to assess individual variation in habitat selection among adult chimpanzees during a 10-year period, testing predictions about trade-offs between foraging and reproductive effort. We found that nonswollen females selected the highest-quality habitats compared with swollen females or males, in line with predictions based on their energetic needs. Swollen females appeared to compromise feeding in favor of mating opportunities, suggesting that females rather than males change their ranging patterns in search of mates. Males generally occupied feeding habitats of lower quality, which may exacerbate energetic challenges of aggression and territory defense. Finally, we documented an increase in feeding habitat quality with community residence time in both sexes during the dry season, suggesting an influence of familiarity on foraging decisions in a highly heterogeneous landscape.

**Key words:** animal ecology, environmental heterogeneity, habitat selection, primate behavior, species distribution models.

## INTRODUCTION

Although animals select habitats based on a complex interaction of factors including the distribution of predators, competitors, and abiotic properties of the environment (Tews et al. 2004), the availability of food resources is undoubtedly one of the most fundamental factors shaping animal distribution, abundance, ranging, and

grouping patterns (rodents: Bergallo and Magnusson 1999; birds: Karr 1976; Holmes and Schultz 1988; primates: Stevenson 2001; Chapman et al. 2004). The influence of food availability on behavior has received particular attention among primates and has been considered one of the main evolutionary factors selecting for variation in primate social organization (Wrangham 1980; Sterck et al. 1997). Multiple dimensions of food availability exist, including quantity, quality (Chapman et al. 2003), spatial distribution (Oates 1987; Isbell et al. 1998), and temporal variability (Vogel and Janson 2011). Each of these aspects of food availability can influence

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behavior and life history in multiple ways, the understanding of which is a fundamental goal in behavioral ecology.

On larger spatial scales (e.g., landscape or regional level), food availability is rarely assessed directly. Instead, suitable habitats are identified a priori based on knowledge of a species' habitat preferences (e.g., Schadt et al. 2002) or based on occurrence and density data that are then linked to land cover classifications derived via remote sensing and image classification techniques (e.g., Peck et al. 2011). As plant species composition cannot readily be inferred using remote sensing methods, land cover assessments are not well suited to understanding small-scale patterns of habitat selection and within-habitat variation in resource distribution that influences animal behavior and ranging. Such small-scale variation at local scales can be considerable, however (Ovaskainen 2004; Dunn and Majer 2007), and be a driving factor in animal distribution across the landscape (marsupials: Murray, Low Choy, et al. 2008; rodents: Orrock et al. 2000; primates: Rovero and Struhsaker 2007; birds: Seoane et al. 2006). Therefore, small-scale habitat heterogeneity is of particular relevance for understanding behavioral adaptations among selective feeders with pronounced dietary preferences for a subset of available plant foods, such as most primates (Milton 1993).

To estimate food availability on smaller spatial scales, perhaps the most common method in primate behavioral ecology is to conduct vegetation surveys in which presence and basal area are recorded in randomly or semirandomly located plots. The total basal area of specific food species can give an estimate of its abundance (Chapman et al. 1992), and multiple species can be combined to estimate total availability of food in an area of interest (Newton-Fisher et al. 2000; Mitani et al. 2002). This approach is frequently used to calculate indices of food abundance and their temporal variation, in conjunction with the monitoring of tree phenology (Fashing 2001; Savini et al. 2008; Foerster et al. 2012). How accurately these indices can reflect spatial variation in habitat quality depends not only on sample size (area of plots relative to study area or habitat being assessed) but also on the heterogeneity of the habitat. The proportion of study area sampled by vegetation plots is generally very small, with common values for field studies of nonhuman primates ranging between <1% and 2% (~2%: Behie et al. 2010; ~0.5%: Chapman et al. 2015; ~1%: Mitani et al. 2002; ~0.1%: Rudicell et al. 2010; ~0.5%: Sterck 1997). Therefore, reliable estimation of habitat quality with the plot method is limited to either relatively homogeneous areas and/or large spatial scales such as home ranges, habitat types, or entire study areas, which may result in biased estimates of habitat quality (Mitchell and Powell 2008).

Unfortunately, increasing the spatial resolution of habitat quality measures by increasing plot sampling effort is unfeasible in most scenarios due to constraints on time and human resources. An alternative approach may lie in the prediction of species occurrences outside of vegetation plots, given a combination of environmental factors that characterize known presence locations. Making such predictions is precisely the goal of species distribution models (SDMs) (Elith and Leathwick 2009).

Various types of mathematical models have been used in SDMs, including random forest regression and classification trees (Liaw and Wiener 2002), maximum entropy models (MaxEnt) (Phillips et al. 2006), BIOCLIM (Busby 1991), Domain (Carpenter et al. 1993), and GARP (Stockwell 1999). MaxEnt has become one of the most popular SDMs for understanding current species distribution (Tinoco et al. 2009), forecasting future distribution under climate change scenarios (Elith et al. 2011), predicting invasive species distribution (Ward 2007), and for other landscape ecology applications. Requiring presence-only species data, MaxEnt has superior predictive power even with small sample

sizes (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008) and model performance is relatively unaffected by sample size variation and data subsampling (Phillips et al. 2006). For that reason, MaxEnt models are particularly well suited to model the distribution of target species in the absence of systematic surveys. Given the spatial extent of predictions and relatively coarse environmental input data available in many parts of the world, MaxEnt models have most often been applied at spatial resolutions of 1 km or above, with a few recent exceptions (Keinath et al. 2010; Laporta et al. 2012; Amici et al. 2014). Empirical work has demonstrated, however, that smaller-scale resolutions in habitat characteristics are useful for predicting animal distribution and abundance in heterogeneous environments (Pettorelli et al. 2001; Rovero and Struhsaker 2007), and inform our understanding of animal movements across the landscape (Boettiger et al. 2011; Avgar et al. 2013).

Our study has 4 main objectives. We first test how well MaxEnt SDMs of vegetation plot data can predict small-scale variation of important plant food species consumed by wild chimpanzees (*Pan troglodytes*) at Gombe National Park, Tanzania. Second, we combine the resultant food species distributions with information on each species' relative dietary importance in order to create a high-resolution feeding habitat quality surface. Third, we assess how feeding habitat quality varies by broad vegetation class, elevation, and latitude, 3 important ecological gradients in our study system. Finally, we apply our method to the examination of individual differences in feeding habitat selection in relation to sex and reproductive state to better understand the trade-offs between foraging and reproductive effort in chimpanzee behavior.

The fission–fusion social organization (Kummer 1971; Aureli et al. 2008) of chimpanzees, in which subgroups (known as parties) frequently change size and composition within and between days (Nishida 1968; Goodall 1986), is thought to allow individuals to better cope with spatiotemporal variation in resource distribution and resulting feeding competition (Wrangham 1979; Symington 1990; Lehmann et al. 2007). Previous research has shown that party size is sensitive to resource abundance and distribution (e.g., Chapman et al. 1995; Boesch 1996; Murray et al. 2006) and that individuals in larger parties spent less time in feeding (Wrangham 1977). These findings suggest that energetic considerations play an important role in chimpanzee space use and social dynamics.

Given their greater energetic investment into reproduction (Trivers 1972), females are expected to prioritize feeding and maximize their feeding efficiency whenever possible. Indeed, females at Gombe and elsewhere in eastern African populations tend to forage alone or in small parties, which is thought to minimize feeding competition (Wrangham 1979). Female core areas vary in quality (Newton-Fisher et al. 2000; Murray et al. 2006; Emery Thompson et al. 2007; Kahlenberg et al. 2008), and this variation may be responsible for rank-related variation in body mass (Pusey et al. 2005) and measures of reproductive success (Pusey et al. 1997). In contrast to females, male chimpanzees form larger parties, move longer distances (Wrangham and Smuts 1980; Chapman and Wrangham 1993; Bates and Byrne 2009), and aggressively defend community boundaries (Goodall 1986; Herbinger et al. 2001; Watts and Mitani 2001). Diverging theories exist about whether males actively search for females or move about primarily in search of food and territory defense (Williams et al. 2004; Newton-Fisher 2014), but empirical evidence suggests that both range defense and competition for mates come at a significant energetic cost (Amsler 2010; Georgiev et al. 2014).

Given the sex-specific reproductive strategies outlined above, we expected that nonswollen female range use would be most focused on areas of high feeding quality, compared with either swollen, sexually receptive females or males. As male movements are known to be longer and more linear compared with females (Bates and Byrne 2009), they are likely to traverse a greater range of habitats

that includes both low- and high-quality feeding locations. Swollen females spend more time in mixed-sex parties and move longer distances than nonswollen females (Williams, Liu, et al. 2002), and therefore, their habitat selection may fall in between that of males and nonswollen females. Particular foraging strategies may counteract the expected differences in feeding habitat quality depending on details of food distribution and feeding competition. For example, energetic demands and larger party sizes may force males to select even higher-quality feeding habitats than females, forego feeding in between high-quality patches, and even displace females from the best feeding sites. However, if few food patches can accommodate larger male or mixed-sex parties, these parties may be forced to include lower-quality feeding habitats to minimize feeding competition and sustain energy intake throughout the day, further decreasing the relative feeding habitat quality for males below that of females.

## METHODS

### Study system

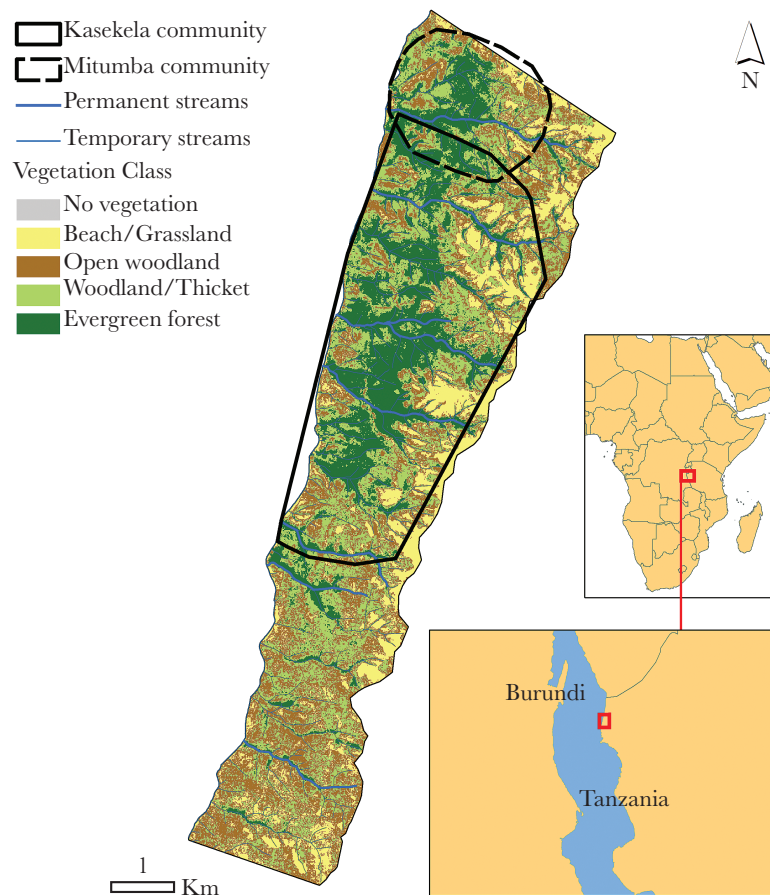
Our study area is the Gombe National Park in western Tanzania (Figure 1). Protected since the early 1940s (Moreau 1945), the area gained international attention through the ground-breaking behavioral studies of chimpanzees conducted by Goodall (1986) since 1960, and continued to this day by a collaborative team of scientists (Wilson 2012). Currently, the 35 km<sup>2</sup> area is home to 90–100 chimpanzees in 3 communities, 2 of which—Kasekela (KK) and

Mitumba—are the subject of long-term behavioral and ecological research, and a third that has been monitored regularly because circa 1999 but remains unhabituated.

Elevation in the park rises from 766 m above sea level along the shores of Lake Tanganyika to 1622 m along the ridge that forms the eastern boundary of the park. The terrain is complex, with numerous steep valleys and ridges traversing the park in predominantly east-west direction. Vegetation cover changes distinctly from south to north and east to west (Figure 1). Dense forests are mainly located in the central and northern parts of the park, especially concentrating in the valleys at lower elevations. The eastern, higher elevations of the park are generally covered by shrubs, grasslands, and bare lands (Pintea 2007).

Gombe experiences a distinct dry season between May and October (Clutton-Brock and Gillett 1979), which is associated with leaf loss among deciduous trees distributed mostly in the southern parts of the park and at higher elevations away from water sources. Mean annual rainfall for the period 1970–2014 is an estimated 1190 mm (Schneider et al. 2011), with June/July being the driest months (6 mm mean monthly precipitation), and November–January being the wettest months (178 mm mean monthly precipitation).

The diet of chimpanzees at Gombe is diverse, with >135 identified plant food species recorded to date in our long-term database. Species vary in their temporal availability both within and across years, as is typical for other tropical forests (van Schaik and Pfannes 2005). Overall, the wet season likely provides more abundant and/or higher-quality food, as indicated by greater average body mass



**Figure 1**

Overview of study area, with main land cover classes, stream locations, and boundaries for 2 study communities of chimpanzees as estimated with 99% minimum convex polygons for recorded sightings for the period 2000–2009.

(Pusey et al. 2005) and the tendency to form larger parties (Murray et al. 2006). However, there is considerable variation across years in the relative importance of fruits in the diet during wet and dry season months (Foerster S, unpublished data).

## Vegetation surveys

Our vegetation data included survey plots and phenological transects. C.M.M. and M.L.W. and D.M. worked with assistants to establish 241, 20×20 m<sup>2</sup> vegetation plots that were randomly distributed throughout the range (C.M.M. plots, *N* = 150, 2004; M.L.W./D.M. plots, *N* = 91, 2005–2007) and that covered about 0.28% of the study area (Figure S1, Supplementary Materials I). The C.M.M. plots recorded the 10 most commonly consumed tree species that accounted for a yearly average of 48.7% of the vegetation diet, along with their diameter at breast height (DBH; measured 137 cm above ground) (Murray et al. 2006). The M.L.W. plots were stratified and distributed randomly within cover type (evergreen forest/vine tangle, thicket woodland, open woodland, grassland) (Rudicell et al. 2010). In contrast to the previous survey, all trees >10 cm DBH were identified by their local name and species, if possible. All plots counted shrubs and vines regardless of DBH within a 5×5 m<sup>2</sup> subplot. For species not recorded in the C.M.M. survey, none of the C.M.M. locations entered our modeling. In addition, phenology transects were established from 1997 to 2007 to record temporal changes in food availability, in which 261 chimpanzee food trees including 14 species were marked along easily accessible trails. Given their nonrandom distribution, we avoided using these location records except for species that were recorded on <40 vegetation survey plots (see below).

Among all food species recorded in the above vegetation mapping, we identified target food species to be included in our modeling if they contributed at least 1% of the chimpanzee diet in 1 or more seasons during our study period (see below for calculations), and if at least 10 presence locations were available for the species, which is considered a minimum sample size for acceptable model performance (Wisiz et al. 2008). These criteria resulted in a final list of 24 food species (Table 1), which together accounted for about 75% of all plant feeding time during the study period.

## Environmental input data

We included raster layers of 11 environmental variables (Figure 2) and 1 mask layer (see below) in our models to predict species occurrence. An elevation raster was derived from the digitization of elevation contours from 1:50,000 topographic maps using the TOPOGRID function in ArcInfo, at a spatial resolution of 10 m (Pintea 2007). Using the ArcGIS Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014), we derived the following predictors from the elevation raster, at the same resolution: aspect, slope, surface curvature (concavity/convexity) index (Bolstad and Lillesand 1992), heat load index (McCune and Keon 2002), surface relief ratio (Pike and Wilson 1971), and compound topographic index (Gessler et al. 1995). To constrain model predictions to vegetated areas, we included 2 vegetation layers: 1) a Normalized Difference Vegetation Index (NDVI), calculated from Landsat TM5 Surface Reflectance Climate Data Records collected on 14 June 2005, and resampled from 30- to 10-m resolution to match all other environmental layers and 2) a land cover map derived from 2001 IKONOS satellite imagery (Pintea 2007) to constrain predictions for each species to one of the following land cover classes: evergreen forest (887 ha), woodland/thicket (1189 ha), open woodland (851 ha), beach/grassland (599 ha), and bare ground (2.9 ha).

This map was aggregated from 4- to 10-m resolution. Lastly, we included 2 layers with the distance from the center of each grid cell to the nearest temporary or permanent stream as indicators of water availability.

## Model construction and performance

There are 2 stages in the process of species distribution modeling: model training and model prediction. In the model training stage, species presence locations are combined with randomly sampled “pseudo” absence locations from the study area. The MaxEnt algorithm then trains a model that best distinguishes presence from pseudo absence locations using the environmental predictors provided. In the second step, this model is then used to predict the probability of presence at any other location.

Although vegetation survey locations were chosen as randomly as possible across the park, their distribution was concentrated in the western parts of the park that were most often used by chimpanzees as feeding areas. Phenology locations, on the other hand, were distributed along trails and thus not randomly spread over the area at all. To avoid biasing model predictions (Elith et al. 2011), we applied a mask that restricted the model training algorithm to sample background data from the region that was covered by vegetation surveys or phenology transects. This mask was included as a 12th environmental variable layer (Figure 2), with values of 0/1 for not sampled and sampled areas, respectively. The model built from these training data was then extrapolated to predict species distribution throughout the park. As for some environmental variables the value ranges in the training data were smaller than the full range measured throughout the park (e.g., elevation), we used “clamping” to constrain values in the prediction models to the upper or lower limits of the training data (Phillips et al. 2006). All modeling was done using MaxEnt v.3.3.3 (Phillips et al. 2006; Elith et al. 2011).

We used a cross-validation method to minimize over-fitting and reduce model variances. For this, the presence data were split into 10 random folds. In each model run, 9 random folds were used as input data for model training. In the next run, one of the 9 data folds was replaced with the previously withheld data to make model predictions. This process was repeated 10 times until all 10 folds were withheld from model training once. The default prediction by MaxEnt is a numerical habitat suitability value for each species, ranging from 0 to 1 (Elith et al. 2011). Model-predicted habitat suitability values for each species were averaged across the 10 random draws to obtain a mean habitat suitability value per species per 10-m grid cell.

As an indicator of model performance, we report the area under the receiver-operating characteristic curve (AUC) (Fielding and Bell 1997); an AUC above 0.75 indicates that the SDM is potentially useful (Elith 2000). As the default cross-validated AUC calculated by MaxEnt uses “pseudo absence” data sampled randomly from the masked study area (see above) and may therefore contain confirmed presence locations, we calculated our own AUC with confirmed absence locations and the full set of presence locations recorded for a given species.

To create species distribution maps, we binarized MaxEnt suitability values in each 10×10 m<sup>2</sup> grid cell, indicating predicted presence or absence in that location. An optimal threshold for this classification was determined empirically as the value that maximized the sum of model sensitivity (true positive rate) and specificity (true negative rate) for a given species (Cantor et al. 1999; Manel et al. 2001). This threshold method is considered effective



**Table 1**

**List of modeled plant food species, number of presence locations on plots and phenology transects, number of confirmed absence locations, relative importance in the diet across the entire study period (2000–2009), and maximum relative importance in the diet during any given 6-month period (season), sorted in the order of dietary importance**

Species name (local name)	Plots	Transect	NP	NA	Mean % in decade	Maximum % of seasonal diet
<i>Parinari curatellifolia</i> (Mbula)	64	0	64	174	11.31	44.29
<i>Saba comorensis</i> var <i>florida</i> (Mabungo makubwa)	83	0	83	149	10.48	24.49
<i>Landolphia lucida</i> (Mabungo madogo)	127	0	127	112	9.19	25.56
<i>Monanthotaxis poggei</i> (Budyankende)	167	0	167	72	6.42	21.65
<i>Elaeis guineensis</i> (Ngazi)	25	32	57	207	5.7	12.2
<i>Ficus</i> sp.	23	37	60	194	5.6	9.4
<i>Pterocarpus tinctorius</i> (Msiloti)	22	0	22	210	5.36	10.91
<i>Pseudospondias microcarpa</i> (Mgwiza)	49	0	49	190	4.87	17.19
<i>Vitex fischeri</i> (Mpapa)	63	0	63	175	3	11.42
<i>Baphia capparidifolia</i> (Nkonzi)	52	0	52	187	2.94	6.32
<i>Garcinia huillensis</i> (Msalasi)	28	17	45	207	1.65	6.11
<i>Harungana madagascariensis</i> (Mshaishai)	10	15	25	81	1.57	9
<i>Diplorhynchus condylocarpon</i> (Msongati)	118	0	118	120	1.49	4.95
<i>Grewia platyclada</i> (Rukungu)	10	20	30	78	1.19	6.65
<i>Syzgium guineense</i> (Mgege)	8	18	26	79	1.15	8.62
<i>Mellera lobulata</i> / <i>Hypoestes verticillaris</i> (Kitota)	74	0	74	165	0.6	1.87
<i>Sabicea orientalis</i> (Bulindankwavu)	11	19	30	80	0.55	3.09
<i>Uapaca nitida</i> (Mhandehande)	3	20	23	85	0.53	4.92
<i>Antidesma venosum</i> (Mziganziga)	34	0	34	57	0.5	2.31
<i>Canthium hispidum</i> / <i>venosum</i> (Mtabungwa)	36	19	55	55	0.5	1.97
<i>Antiaris toxicaria</i> (Mwinamila)	6	7	13	82	0.25	2.37
<i>Pterocarpus angolensis</i> (Mninga)	19	29	48	72	0.18	1.09
<i>Salacia leptoclada</i> (Mabungo makavu)	29	0	29	62	0.1	0.75
<i>Annona senegalensis</i> (Mtopetope)	36	0	36	55	0.04	0.34

NA, number of confirmed absence locations; NP, number of presence locations.

for enhancing model performance (Liu et al. 2005). Sensitivity, specificity, and the average accuracy (AA) calculated across those 2 measures serve as additional indicators of model performance. All model performance statistics were calculated with the “ROCR” R package (Sing et al. 2005; R Core Team 2014).

## Behavioral data

Behavioral data were collected by teams of Tanzanian field assistants and external researchers, who conducted almost daily all-day focal animal samples on identified individuals (Goodall 1986). During these focal observations, group composition was monitored in intervals of 15 min, and the location of the party was mapped at each interval with an approximate spatial accuracy of 100 m. In addition, for all females observed during focal follows, observers recorded the presence and size of the female's sex skin (i.e., perineal) swelling, which indicates sexual receptivity, as flat, quarter swollen, half swollen, three-quarters swollen, and fully swollen. All feeding bouts of the focal individual were recorded with start and end times, food type, and species name if known. From this dataset, we calculated the relative proportion of feeding time that each species accounted for in a given season, by summing all feeding bout durations for a given species across all focal observations and dividing by the total duration of all feeding bouts in that season.

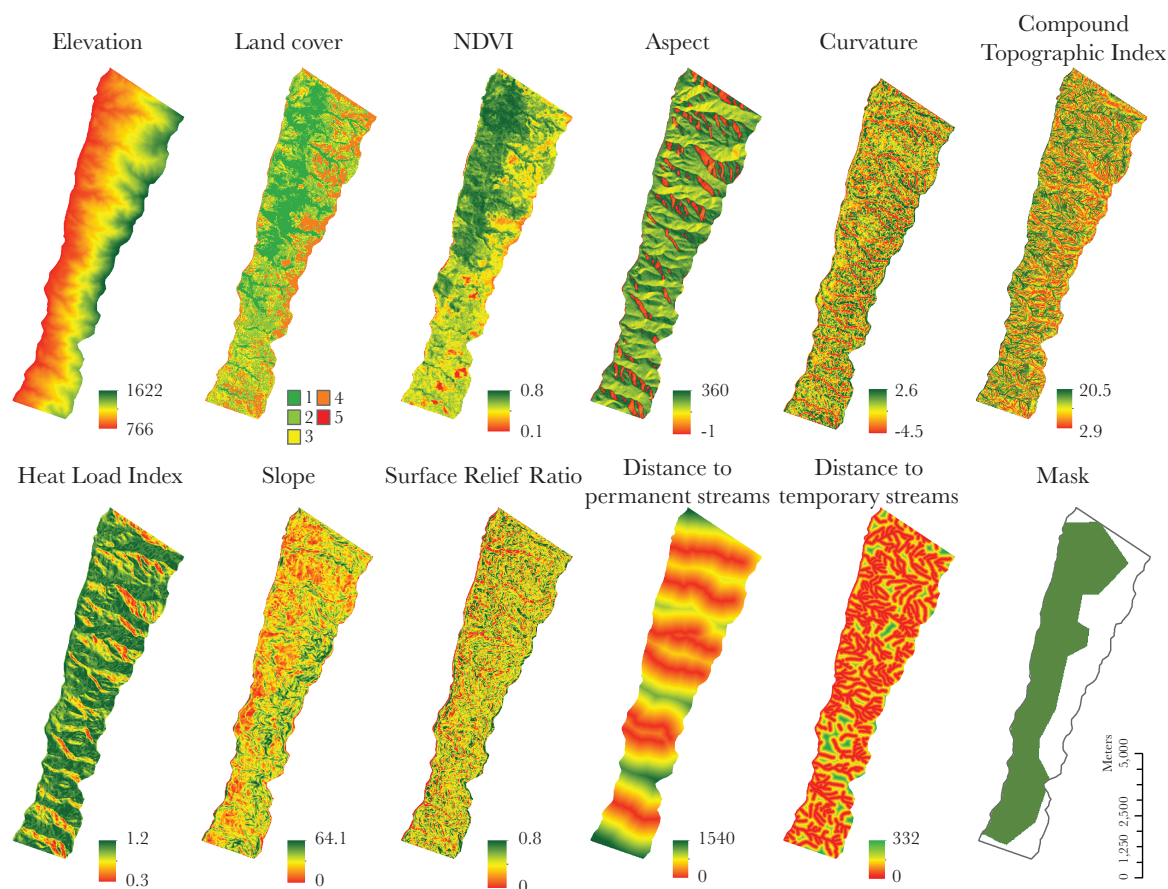
## Habitat quality surface

The 24 modeled food species vary considerably in their relative importance in the diet, both within and across time periods. Therefore, to obtain an estimate of habitat quality, we summed up the proportions of feeding time across all species predicted to occur in a given  $10 \times 10 \text{ m}^2$  grid cell, separately for each wet and dry season (November–April and May–October, respectively). By doing so,

we created multiple quality surfaces that each estimate the relative importance of locations as feeding habitat for chimpanzees in a specific season, based on all available feeding records. All raster calculations were performed with the “raster” package in R (Hijmans and van Etten 2012). To obtain the most accurate estimates of habitat quality, here we focus on a 10-year period (2000–2009) during which both vegetation survey data and detailed feeding records were collected. As intercommunity differences were not among our main objectives, our models quantify variation in feeding habitat quality across Gombe for members of the KK community only.

## Statistical analyses

To test for individual differences in habitat quality related to sex and reproductive state, we used general linear mixed model analyses. Individual identity was entered as random effect, habitat quality at sighted location as dependent variable, and as fixed effect predictors, we used season (dry/wet), sex, and whether or not a female was fully swollen. In chimpanzees, female sexual receptivity and mating are almost entirely restricted to fully swollen periods (Goodall 1986). We combined sex and swelling state into 1 categorical predictor with 3 levels: males, nonswollen females, and swollen females. We included all individuals who were at least 12 years old on the day of observation, which approximates the minimum age at which known-aged females at Gombe have given birth (Pusey A, unpublished data), and at which males have sired offspring (Wroblewski et al. 2009). As our habitat quality relates to dietary importance, we limited our dataset to all locations at which the focal individual was feeding (i.e., feeding parties). Although the proportion of individuals in a party who are feeding is known to vary (Wrangham 1977), previous analyses of simultaneous focal observations in the same party showed that the average likelihood



**Figure 2**  
Environmental layers used for modeling chimpanzee plant food species distribution.

of cofeeding is about 78% (Miller et al. 2014). Furthermore, we assume that no systematic bias exists in how this proportion varies with sex and reproductive state. We entered residence time in the community (actual age in years for natal individuals, years spent in community for those who immigrated) as a continuous covariate, because increased familiarity with an area can influence foraging decisions (Wrangham 1977; Murray, Gilby, et al. 2008). As seasonal differences in food availability and distribution are pronounced at Gombe (Wrangham 1977; Goodall 1986; Murray et al. 2007), we considered the possibility that patterns of habitat selection vary between wet and dry season, and therefore included an interaction effect between season and all other predictor variables in our full model. As we are specifically interested in the joint effects of all included predictor variables, we did not conduct model selection and report the results from our full model only. Analyses were conducted in IBM SPSS Statistics for Windows, Version 21.0 (IBM Corp., Armonk, NY).

## RESULTS

### Model performance

Despite lacking data on spatial variation in 2 important predictors of plant distribution (rainfall and soil properties), our models performed well on most of the 24 plant food species (Table 2). The average AUC of model-predicted suitability across 24 species was  $0.87 \pm$  standard deviation (SD) 0.07, with only one species (*Antidesma*

*venosum*) falling below 0.75. Sensitivity and specificity averaged  $0.84 \pm$  SD 0.10 and  $0.79 \pm$  SD 0.13, respectively (AA:  $0.81 \pm$  SD 0.07), indicating that presence and absence locations were about equally well predicted across all species. Of the 24 plant species modeled, 18 species had AUC and overall prediction accuracies of  $>0.75$  and 75%, respectively, and 6 species had AUC and mean accuracy of  $>0.90$  and  $>85\%$ , respectively. According to jackknife tests of the modeling results, NDVI was the most important predictor variable for 9 species, followed by elevation (6 species), land cover (5 species), distance to permanent streams (3 species), and aspect (1 species).

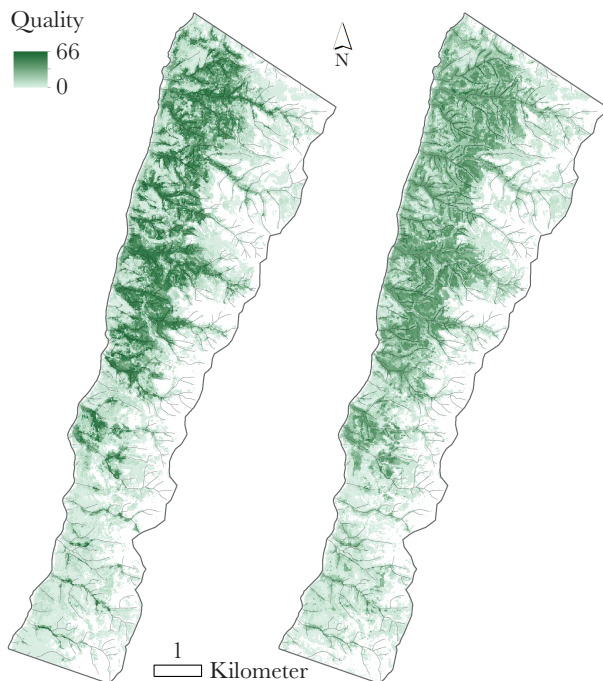
### Variability of habitat quality across and within landcover classes

Of the 24 species modeled, evergreen forest locations contained a mean of  $8.3 \pm$  SD 3.5 species, followed by woodland/thicket ( $3.9 \pm$  SD 3.2) and open woodland ( $2.1 \pm$  SD 1.9) (Figure S2, Supplementary Materials I). The mean predicted number of species for other land cover classes was zero.

Combining predicted species distributions (Supplementary Materials II) with the relative importance of each species in the diet allowed us to assess variation in feeding habitat quality for chimpanzees on a small spatial scale separately for individual seasons (Figure 3). Averaging across all seasons, evergreen forest obtained the highest average quality as chimpanzee food habitat across all years (mean cumulative sum of feeding proportions per grid cell:  $33.4 \pm$  SD 16.3,  $N = 88,705$  grid cells), followed by

**Table 2****MaxEnt model performance statistics, accuracy assessments of predicted species distributions, and most important environmental predictor variable**

Species	AUC	Sensitivity (true positive)	Specificity (true negative)	AA <sup>a</sup>	Top predictor variable <sup>b</sup>
<i>Uapaca nitida</i>	1	1	0.99	0.99	ELEVATION
<i>Antiaris toxicaria</i>	0.98	0.92	0.98	0.95	NDVI
<i>Sabicea orientalis</i>	0.95	0.87	0.91	0.89	ELEVATION
<i>Grewia platyclada</i>	0.93	0.8	0.91	0.86	PSTREAMS
<i>Pseudospondias microcarpa</i>	0.92	0.84	0.87	0.86	LCOVER
<i>Syzgium guineense</i>	0.93	0.77	0.95	0.86	PSTREAMS
<i>Annona senegalensis</i>	0.88	0.83	0.86	0.84	ELEVATION
<i>Baphia capparidifolia</i>	0.88	0.89	0.79	0.84	LCOVER
<i>Ficus</i> sp.	0.89	0.8	0.86	0.83	NDVI
<i>Pterocarpus tinctorius</i>	0.87	0.91	0.76	0.83	ASPECT
<i>Salacia leptoclada</i>	0.9	0.86	0.81	0.83	LCOVER
<i>Harungana madagascariensis</i>	0.86	0.88	0.77	0.82	ELEVATION
<i>Pterocarpus angolensis</i>	0.85	0.84	0.78	0.81	LCOVER
<i>Diplorhynchus condylocarpon</i>	0.88	0.7	0.9	0.8	NDVI
<i>Elaeis guineensis</i>	0.88	0.95	0.66	0.8	NDVI
<i>Landolphia lucida</i>	0.86	0.87	0.73	0.8	NDVI
<i>Monanthotaxis poggei</i>	0.86	0.95	0.65	0.8	NDVI
<i>Canthium hispidum/venosum</i>	0.83	0.78	0.76	0.77	NDVI
<i>Mellera lobulata/Hypoestes verticillaris</i>	0.84	0.92	0.62	0.77	PSTREAMS
<i>Vitex fischeri</i>	0.77	0.76	0.69	0.73	LCOVER
<i>Antidesma venosum</i>	0.74	0.88	0.56	0.72	ELEVATION
<i>Garcinia huillensis</i>	0.76	0.93	0.5	0.72	NDVI
<i>Saba comorensis</i> var. <i>florida</i>	0.78	0.68	0.74	0.71	NDVI
<i>Parinari curatellifolia</i>	0.75	0.55	0.83	0.69	ELEVATION

<sup>a</sup>Calculated as simple mean over sensitivity and specificity.<sup>b</sup>LCOVER: main land cover classes as determined from a 2000 vegetation classification (see text for details); PSTREAMS: distance to permanent streams.**Figure 3**

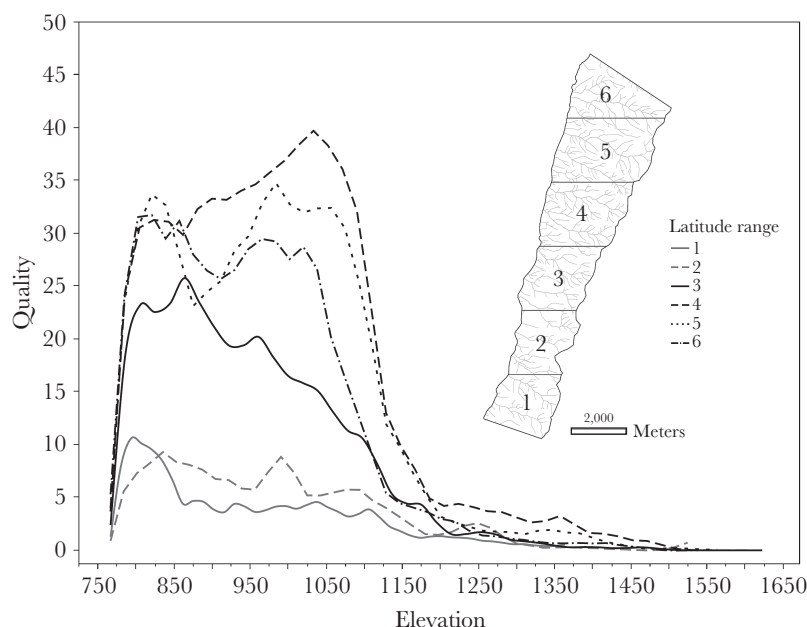
Example chimpanzee habitat quality layers in wet (left) and dry (right) season of 2006, at a spatial resolution of 10 m. Values represent the sum of proportions of feeding time across all modeled food species that were predicted to occur in a given grid cell.

woodland/thicket ( $10.5 \pm \text{SD } 11.8$ ,  $N = 118934$ ) and open woodland ( $3.2 \pm \text{SD } 5.6$ ,  $N = 85138$ ). Very low quality was predicted for beach/grassland ( $0.6 \pm 2.5$ ,  $N = 59868$ ) and bare ground ( $0.6 \pm \text{SD } 2.1$ ,  $N = 287$ ), as expected.

Habitat quality varied considerably across locations within the same land cover class. To allow comparison of variance across classes with different means, we expressed this variability using the coefficient of variation (CV). Evergreen forest had the least variable quality ( $\text{CV} = 0.49$ ), followed by woodland/thicket ( $\text{CV} = 1.12$ ) and open woodland ( $\text{CV} = 1.77$ ). Spatial variation in habitat quality within land cover classes was slightly more pronounced in wet than dry season within open woodlands ( $\text{CV} = 2.14$  vs.  $1.79$ , respectively) and woodlands/thickets ( $\text{CV} = 1.29$  vs.  $1.12$ ), but the variability of quality in evergreen forest remained stable over time ( $\text{CV} = 0.52$  in both wet and dry season). The mean quality of open woodlands increased from wet to dry season ( $1.9 \pm \text{SD } 4.1$  vs.  $4.26 \pm \text{SD } 7.8$ ), as did the quality of woodland/thicket ( $9.25 \pm 11.9$  vs.  $10.4 \pm 11.7$ ). In contrast, the mean quality of evergreen forest decreased ( $34.4 \pm 18$  vs.  $26.6 \pm 13.8$ ), indicating a shift toward feeding on plant food items outside the evergreen forest during the dry season.

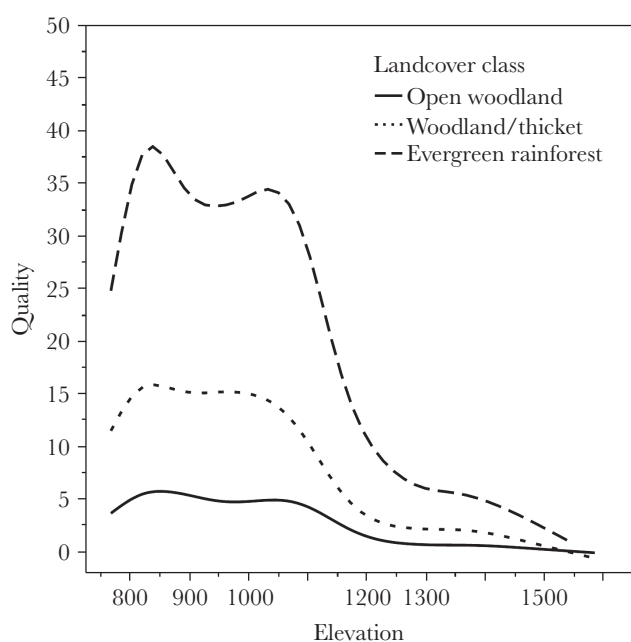
### Variability of habitat quality with elevation and latitude

As indicated by its influence on model predictions (see above), elevation had a major influence on feeding habitat quality throughout the park. Regardless of latitudinal position, quality decreased with increasing elevation. At the same time, high elevation was essential for maintaining forest in the central and northern portions of the park due to orographic (mountain-caused) rainfall. There was considerable variation in the elevation–habitat quality relationship depending on latitude (Figure 4). In the northern parts of the park, habitat quality increased sharply within the first 100 m above baseline altitude at the shores of Lake Tanganyika, and remained consistently high to about 1000–1100 m above sea level. In contrast, habitat quality decreased gradually above a threshold of about 850 m in the southern parts of the park. The relationship between



**Figure 4**

Change in mean habitat quality with elevation, for 6 arbitrary latitudinal ranges throughout Gombe National Park. Curves are smoothed interpolation lines ( $\lambda = 100$ ) across all 10-m grid cells of a given elevation in each latitudinal range, as defined on the inset map.



**Figure 5**

Change in mean habitat quality with elevation (meters above sea level) within each of 3 main land cover classes used as feeding habitats of chimpanzees at Gombe. Curves are smoothed interpolation lines ( $\lambda = 100$ ) across all 10-m grid cells of a given elevation in each land cover class.

elevation and habitat quality was not confounded by latitudinal changes in land cover; within each of the 3 main land cover classes, habitat quality decreased with elevation, with evergreen forest showing the greatest overall change in quality along the elevation gradient (Figure 5). The elevation gradient of quality was similar across seasons.

### Individual differences in feeding habitat quality

Sex, female swelling state, and residence time had significant influences on feeding habitat selection (Table 3, Figure 6). Regardless of season, males were recorded at lower-quality feeding locations than females, and nonswollen females were recorded at the highest-quality locations (estimated marginal mean  $z$ -score:  $-0.075 \pm$  standard error [SE]  $0.016$  for males vs.  $-0.005 \pm$  SE  $0.014$  for swollen females vs.  $0.057 \pm$  SE  $0.013$  for nonswollen females). Independent of sex and female swelling state, mean feeding habitat quality consistently increased with residence time during the dry season months but not in the wet season (Table 3).

### DISCUSSION

Methods for estimating spatial variation in the quality of animal habitats have often relied on a limited number of vegetation survey plots or transects or on relatively coarse vegetation type assessments based on ground surveys or satellite imagery. These methods are likely to underestimate spatial heterogeneity of habitats and home ranges, yet the small-scale variation in habitat features can be an important driver of animal space use patterns and affect reproductive success (Pettorelli et al. 2001; Williams, Marsh, et al. 2002; Rovero and Struhsaker 2007; Brambilla and Ficetola 2012). To improve our understanding of chimpanzee space use, we applied one of the most widely used species distribution modeling approaches to a typical vegetation survey dataset that covered a very small proportion of the study area only, with the goal of estimating feeding habitat quality across the study area at a small spatial scale.

### Model performance

We created food plant suitability and distribution maps for the most important plant food species for chimpanzees at Gombe. Despite lacking information about within-site variability in soil properties and



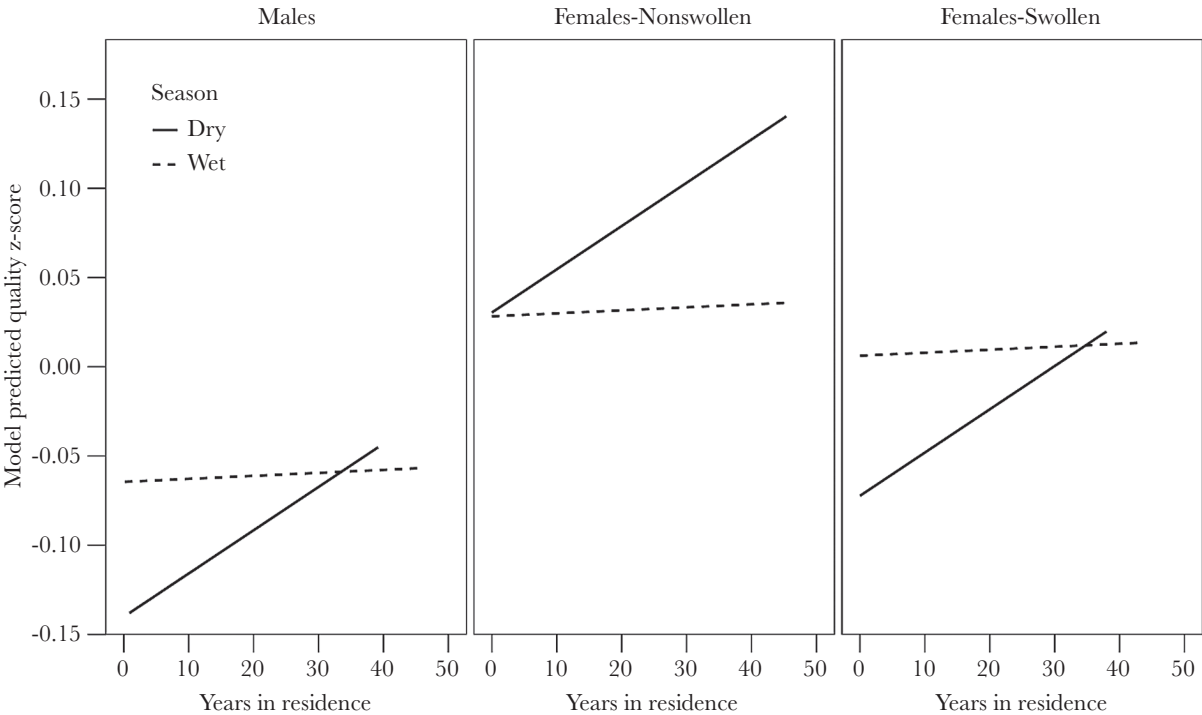
rainfall as important environmental factors for plant growth (Coudun et al. 2006; Condit et al. 2013), our model performance was similar to what has been achieved by previous studies that used MaxEnt to predict plant species distributions (Hernandez et al. 2006; Phillips and Dudík 2008; Williams et al. 2009; Gogol-Prokurat 2011). Our finding suggests that MaxEnt may be used to predict animal food plant distribution even where data availability is relatively low and limited to globally available datasets such as digital elevation models and remotely sensed NDVI, which proved to be 2 of the most influential environmental predictors in our models. Interestingly, NDVI derived from both Landsat MSS and Landsat ETM+ imagery had previously been shown to correlate positively with time spent feeding for Gombe chimpanzees (Pintea 2007), confirming its relevance as a predictor of plant food distribution in our study system.

Previous studies have demonstrated the effect of sample size on the performance of SDM algorithms (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008). These studies found that compared with most other algorithms, MaxEnt is less sensitive to sample size and retains relatively high predictive power and stability when sample size decreases. Our results are consistent with these findings, as prediction accuracy did not seem to relate closely to sample size across different chimpanzee plant food species. Indeed, we obtained high prediction accuracy for some species despite small sample sizes; examples include *Antiaris toxicaria* ( $N = 13$  presence locations,  $AUC = 0.981$ ,  $AA = 0.968$ ) and *Uapaca nitida* ( $N = 23$ ,  $AUC = 0.998$ ,  $AA = 0.991$ ). Because of its capability in predicting species distribution with small sample sizes, MaxEnt is a valuable tool for modeling food species distributions from limited

**Table 3**  
**Results of general linear mixed models of feeding habitat quality in relation to season, sex, swelling state, and residence time in community**

Parameter	Estimate	SE	df	<i>t</i>	<i>P</i>	95% Confidence interval	
						Lower bound	Upper bound
Intercept	0.0062	0.0166	81.5	0.373	0.71	−0.0268	0.0392
Dry season <sup>a</sup>	−0.0785	0.0095	477 190.3	−8.24	<0.001	−0.0972	−0.0598
Males <sup>b</sup>	−0.0707	0.0186	158.9	−3.8	<0.001	−0.1074	−0.0339
Females nonswollen <sup>b</sup>	0.0221	0.0068	387 919.5	3.226	0.001	0.0087	0.0355
Dry season × males <sup>c</sup>	0.0029	0.0106	487 779.9	0.274	0.784	−0.0179	0.0237
Dry season × females nonswollen <sup>c</sup>	0.0806	0.0104	494 462.1	7.765	<0.001	0.0603	0.101
Residence time in years	0.0002	0.0005	618.1	0.306	0.76	−0.0009	0.0012
Residence time in years × dry season	0.0023	0.0003	488 874	7.338	<0.001	0.0017	0.0029

df, degrees of freedom.  
<sup>a</sup>Compared with wet season.  
<sup>b</sup>Compared with swollen females.  
<sup>c</sup>Compared with swollen females in wet season.



**Figure 6**  
Effect of residence time in community on mean feeding habitat quality at which adult chimpanzees were sighted during the study period, in relation to season, sex, and swelling state. Quality is expressed as a standardized score in relation to the mean quality across all feeding party locations in a given season.

number of vegetation survey locations or for rare species (Kumar and Stohlgren 2009).

It is expected that the accuracy of model predictions can be influenced by niche breadth (Hernandez et al. 2006); for species with narrow ecological niches and constrained geographic ranges, a more well-defined relationship between species presence and environmental variables generally leads to more accurate model predictions. For example, the 6 species in our sample for which models performed very well (AUC > 0.9, average predictive accuracy of presence and absence locations combined >85%) were the ones predicted to occur in well-defined, small areas of the park only (Supplementary Materials II). In contrast, the predicted distributions of 5 species for which AUC fell below 0.8 and average predictive accuracy below 80% were relatively widespread throughout the park, likely indicating a greater tolerance for changing environmental conditions. Nevertheless, the average predictive accuracy for these generalist species was still at acceptably high levels and is unlikely to cause significant biases in the interpretation of findings. In order to improve the model performance for species with wide ecological niches, future studies should aim to include additional environmental variables such as rainfall and soil properties in the model training process whenever available, which could lead to improvements in prediction accuracies for all species.

### Habitat quality variation

We found that evergreen forest provided the relatively highest-quality feeding habitat for chimpanzees at Gombe, based on evaluating about 75% of their plant food diet. It is well known that chimpanzees prefer fleshy fruits whenever available (Wrangham 1977; Conklin-Brittain et al. 1998), and our evidence suggests that evergreen forest provided the most consistent access to this important plant food type in our study community; evergreen areas showed the least amount of variance both within and between seasons. As evergreen forests account for a smaller proportion of area compared with the most dominant habitat type, woodlands/thickets (25% vs. 34%), chimpanzees at Gombe appear to feed on evergreen forest plants disproportionately and preferably compared with other habitat types. These findings are in line with previous analyses showing that NDVI—a measure of photosynthetic activity (greenness) that is high in dense evergreen forest—was correlated with the percent time chimpanzees at Gombe spent feeding (Pintea 2007). Preferences are likely to vary across study sites, however, as the relative quality of different habitats available to chimpanzees depends on specific forest composition and spatiotemporal availability of food. For example, chimpanzees in the Budongo Forest Reserve preferred logged forest, clearings, and edge habitat over all other habitat types, related to variation in the abundance of preferred foods (Tweheyo et al. 2004).

The intricacies of food distribution within and across main vegetation types, also indicated by the high variability of our quality metric within the same general habitat type, highlight the importance of taking into account habitat heterogeneity in studies of chimpanzee behavioral ecology. Findings from other studies support this interpretation (Potts and Lwanga 2014). For example, Furuichi et al. (2001) found that secondary forest supported different numbers of chimpanzees depending on the dominant species and that the presence of multiple vegetation types was crucial for providing consistent access to food across seasons. Reliance on heterogeneous landscapes may be particularly important in marginal habitats with marked seasonal variation in the location of food sources (Kortlandt 1983). Along the same lines, a recent study

documented that variability in forest patch size and shape, combined with the presence of old-growth forest, was most influential for predicting habitat suitability for Western chimpanzees (*Pan troglodytes verus*) (Torres et al. 2010). We hope that future applications of our method for assessing small-scale variation in feeding habitat quality will lead to new insights into determinants of temporal dynamics of habitat use.

### Trade-offs in habitat selection

As predicted based on sex-specific reproductive strategies, nonswollen females selected the highest-quality feeding habitats, followed by swollen females and males. These individual differences persisted regardless of season, but were more pronounced during the dry season, indicating that habitat selection was more differentiated among individuals during that time. Evidence suggests that food availability at Gombe and elsewhere is generally lower during the dry season, indicated by smaller party sizes (Wrangham 1977; Doran 1997; Matsumoto-Oda et al. 1998) and decreases in weight (Pusey et al. 2005; but see Uehara and Nishida 1987), as well as increased diet breadth as a coping response to decreased availability of preferred food sources (Murray et al. 2006). Nonswollen females are expected to be most sensitive to decreases in food availability given the energetic costs of gestation and lactation; the generally smaller feeding parties during the dry season may enable them to feed more often in higher-quality areas alone or with dependent offspring. Finally, the finding that swollen females were observed significantly more often in feeding habitats of lower quality than nonswollen females suggests that females trade feeding efficiency for mating effort. This also supports previous assertions that females rather than males change their ranging patterns for the purpose of mating (Newton-Fisher 2014). However, our analyses were not aimed at distinguishing between females actively searching for males or females simply moving in mixed-sex parties that generally range farther and move through a wider range of feeding habitats.

We found that males used the overall lowest-quality feeding habitats, which is consistent with our hypothesis that larger feeding parties and longer distance movements force males to include lower-quality habitats with less important dietary items. Given a general decrease in feeding time with increasing party size (Wrangham 1977), it may be important for males to choose quantity of feeding sites over quality or select feeding sites that allow a larger number of individuals to feed together without exacerbating feeding competition, that is, sites with dispersed food patches or very large patches (White and Wrangham 1988). In light of these findings, and given the energetic costs of male mating effort, aggression, and territory defense (Georgiev et al. 2014), optimizing foraging efficiency and maintaining positive energy balance could exert considerable selective pressure on male behavioral strategies that warrants further studies.

The reported positive relationship between residence time and feeding habitat quality in both sexes lends support to the hypothesis that familiarity may influence habitat selection, especially in as heterogeneous a habitat as Gombe. As food is more widely distributed in the dry than wet season, it is not surprising that community residence time influenced feeding habitat quality during dry but not wet season months. Previous reports highlight the considerable challenges involved in locating food sources and finding efficient travel routes between them (Wrangham 1977), and these challenges are likely exacerbated when food sources are widely dispersed. Indeed, studies on other social mammals have shown that seniority can come with foraging and social benefits that correlate with fitness (McComb et al.

2001; Brent et al. 2015). Given known relationships between age and rank in both male and female chimpanzees (Murray et al. 2006), further work is planned to examine how rank and residence time may interact to determine habitat selection and foraging decisions.

## Broader implications

We believe that our approach may be successfully applied to quantify plant food species distribution in other study areas, even if geospatial data availability is limited. Global elevation data and satellite imagery are available for free at a resolution of 30 m and can be used to derive the topographic variables and vegetation cover types that served as input layers in our SDMs. We expect that the feasibility, accuracy, and discriminative power of such modeling approaches will provide useful extensions of traditional measures of habitat quality for studies of animal behavior and ecology. In particular, the estimates of small-scale variation in habitat quality that can be obtained with our approach are increasingly recognized as an important predictor of animal distributions at regional scales (Martínez et al. 2003; Murray, Low Choy, et al. 2008). In addition, biodiversity and species conservation tools such as connectivity analyses, conservation prioritization planning, and climate vulnerability assessments will benefit from detailed mapping of animal food resources on multiple spatial scales using similar techniques.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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