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Temporal variation in resource selection of African elephants follows long-term variability in resource availability

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Abstract. The relationship between resource availability and wildlife movement patterns is pivotal to understanding species behavior and ecology. Movement response to landscape variables occurs at multiple temporal scales, from sub-diurnal to multiannual. Additionally, individuals may respond to both current and past conditions of resource availability. In this paper, we examine the temporal scale and variation of current and past resource variables that affect movement patterns of African elephants (*Loxodonta africana*) using sub-hourly movement data from GPS-GSM collared elephants in Etosha National Park, Namibia. We created detailed satellite-based spatiotemporal maps of vegetation biomass, as well as distance from surface water, road and fence. We used step selection functions to measure the relative importance of these landscape variables in determining elephants' local movement patterns. We also examined how elephants respond to information, in locations they have previously visited, on productivity integrated over different temporal scales: from current to historical conditions. Our results demonstrate that elephants choose patches with higher than average annual productivity and grass biomass, but lower tree biomass. Elephants also prefer to walk close to water, roads, and fences. These preferences vary with time of day and with season, thereby providing insights into diurnal and seasonal behavioral patterns and the ecological importance of the landscape variables examined. We also discovered that elephants respond more strongly to long-term patterns of productivity than to immediate forage conditions, in familiar locations. Our results illustrate how animals with high cognitive capacity and spatial memory integrate long-term information on landscape conditions. We illuminate the importance of long-term high temporal resolution satellite imagery to understanding the relationship between movement patterns and landscape structure.

Key words: African Savanna; diurnal cycle; fraction of photosynthetically active radiation; long-term memory; movement patterns; normalized difference vegetation index; satellite imagery; seasonal resource variability; spatial cognition; step selection function; time series analysis.

INTRODUCTION

The relationship between resource availability and wildlife movement patterns is pivotal to understanding species behavior and ecology (Nathan et al. 2008, Schick et al. 2008, Soberon and Nakamura 2009). Individual movement as a response to underlying landscape variables reflects the animal's resource preference in the context of availability. Hence, movement links individual behavior and resource selection (Johnson1980, Panzacchi et al. 2016, Van Moorter et al. 2016). While much work has been done over the past years to relate wildlife movement to resource selection, it is not well understood how the relationship between the individuals' movement patterns and detailed underlying landscape variables changes over time. Resource selection varies temporally, with seasonal and interannual variation in resource availability and with changing internal demands of the individual (Fryxell et al. 2004, 2005, Boone et al. 2006, van Beest et al. 2013, Hurley et al. 2014). Further, resource availability at a given time reflects the cumulative outcomes of the forces (e.g., rainfall, fire, grazing) shaping the state of that resource over previous time frames (days, month, years) (Tsalyuk et al. 2017). Therefore, in species with higher cognitive abilities and capacity for memory, movement response to the landscape may reflect not only the current condition of the

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resource, but also the state of the resource integrated over prior periods. However, little research has examined this relationship, which ranges from an individual's response to the immediate conditions on the landscape to long-term memories of past resource distributions.

Observed long-term patterns of resource selection arise from individuals' repeated movement patterns; an animal incorporates information about its surrounding landscape while moving in a particular direction and speed toward a preferred resource. Movement metrics, such as tortuosity and speed, change with the behavioral mode and the underlying resources consumed (Fryxell et al. 2008, Getz and Saltz 2008, Gurarie et al. 2009, 2016, Ares and Bertiller 2010, Nathan et al. 2012). Individuals are expected to walk faster through a less favorable environment, while they will typically linger in a safer landscape with richer resources (Owen-Smith et al. 2010). For example, movement is slower and more tortuous when foraging, while movement toward a water source is fast and directional (Forester et al. 2007, Fryxell et al. 2008, Ares and Bertiller 2010, Chamaille-Jammes et al. 2013). On the other hand, wildlife exhibit directed movement away from certain stimuli such as predators, human disturbance, or other perceived sources of danger, and move faster in these areas (Douglas-Hamilton et al. 2005). However, more research is needed to connect movement modes to underlying landscape variables to bridge individual movement behavior and resource selection.

Movement of wildlife responds to landscape changes over time, from diurnal to multiannual scales (Fryxell et al. 2008, Leblond et al. 2010, Polansky et al. 2010, 2013, Hooten et al. 2014). On a diurnal cycle, each component of the animal's behavior (e.g., drinking, feeding, resting) follows a particular resource (e.g., water sources, vegetation patch, shade; Forester et al. 2007, Fryxell et al. 2008). For example, optimal foraging models showed that maximization of the ratio between energy intake rate and mortality risk can explain circadian rhythm in movements of bison (Fortin et al. 2015). Byrne et al. (2014) used a dynamic Brownian bridge movement model to demonstrate circadian patterns in the utilization distribution of white-tailed deer within different types of forests. Diurnal movement cycles of African elephants vary with primary productivity of vegetation (Wittemyer et al. 2008). Both diel displacement and movement predictability of elephants increase with forage availability (Polansky et al. 2013). However, further research is needed to understand individual movement behaviors that dictate the interaction between animals and their environment at a fine temporal scale.

On a seasonal scale, how animals respond to the landscape varies with seasonal change in resource availability and with changing internal physiological requirements of the individual (Getz and Saltz 2008, Nathan et al. 2008, Godvik et al. 2009, Hooten et al. 2014). For example, ungulates follow the seasonal spatial distribution of productivity and precipitation (Fryxell et al. 2004, Boone et al. 2006, van Beest et al. 2013). This adaptation to seasonal variation in resource availability is crucial for the individuals' survival and the persistence of ungulate populations (Fryxell et al. 2005, Duffy 2011, Hurley et al. 2014). Conversely, as the availability of a particular resource declines with season, the relative importance of that resource to the animal may increase. For example, in the dry season of semiarid savanna, as the availability of surface water diminishes, water has a more prominent influence on animal movement (Redfern et al. 2003). Similarly, in elephants, habitat preference and diet change with season and region (Loarie et al. 2009*a*,*b*, Bohrer et al. 2014). For example, the proportion of grass in elephants' diet and the size of their home range increase in the rainy season, when individuals are less restricted by water availability (Sukumar 2003, van Aarde et al. 2006, Codron et al. 2006).

Most research on the relationship between animal movement and landscape variables considers forage conditions at one particular time scale. Optimal foraging theory predicts, at each given time, that animal feeding behavior and, subsequently, movement patterns on a fine temporal scale, would follow the instantaneous rate of energy intake relative to the expected intake rate in the surrounding landscape (Pyke et al. 1977, Owen-Smith et al. 2010). However, long-term spatial memory of the landscape enables animals to respond not only to the immediate forage availability, but also to past conditions (Gautestad and Mysterud 2010*a*,*b*, Gautestad 2011, Fagan et al. 2013, Polansky et al. 2015, Oliveira-Santos et al. 2016, Bracis and Mueller 2017). Little research has been done on the time span over which individuals integrate spatial information. In particular, little attention has been paid regarding how far in the past individuals retrieve information in making decisions on where to forage. Examining resource selection in response to current and past forage availability may provide more realistic models of individuals' space use.

African elephants are a good model system to study how past resource availability influences movement patterns and what the time span may be. Elephants have excellent cognitive abilities and long-term spatial memory, which enables them to return to favorable resources (McComb et al. 2001, Hart et al. 2008, Polansky et al. 2015, Fishlock et al. 2016). African savannas are unpredictable with prolonged dry season, where knowledge on the long-term availability of resources is highly advantageous. Since elephants are important ecosystem engineers, multiple feedbacks occur between elephants' behavior and savanna vegetation structure. For example, elephants can enhance vegetation diversity by suppressing tree cover, and promoting seed dispersal and nutrient transport (Goheen et al. 2010, Wolf et al. 2013, Coverdale et al. 2016). On the other hand, dense elephant population may cause vegetation degradation and tree damage (Baxter and Getz 2005, de Beer et al. 2006, Franz et al. 2010). In the last decade elephant populations throughout Africa are in steep decline due to increase in poaching and restriction of their range (Thouless et al. 2016). To better understand the changes in the elephants-savanna vegetation dynamics and to improve land management, it is crucial to quantify the variation in elephant movement response to resources at different temporal scales.

A variety of methods have been proposed to examine how underlying landscape affects movement patterns (Getz and Saltz 2008, Avgar et al. 2013). Resource selection functions (RSFs) characterize the resources an animal chooses relative to the "domain of availability," the proportion of resources that are available to the animal on the surrounding landscape (Boyce 2006). Step selection function (SSF) has been proposed as a powerful technique to characterize the relationship between individual directional movement and resource selection (Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). SSF examines the values of landscape variables at each GPS fix of an individual movement pathway as compared to the values of case-control steps, either taken from the distribution of step length and turning angle of the animal (Thurfjell et al. 2014) or from a parametric distribution (Forester et al. 2009, Avgar et al. 2016). Therefore, the "domain of availability" is defined in SSF as the relative proportion of resources available to the animal in its immediate surroundings at each time step (Boyce et al. 2002, Boyce 2006).

Here, we examine the relative importance of landscape variables in determining movement patterns of African elephants (*Loxodonta africana*) in a semiarid African savanna, Etosha National Park, Namibia, across temporal scales, from diurnal to annual. Specifically, we investigate elephants' responses to the underlying temporal scale over which information on resource availability is integrated. To this end, we used high-resolution telemetry data together with detailed high thematic and temporal resolution landscape information from satellite imagery. In particular, we addressed three questions:

(1) What is the relative importance of landscape variables in determining African elephant movement in Etosha National Park?

In this regard, we examined the relative importance of consumptive resources (vegetation, water) vs. anthropogenic features (roads, fence) in determining elephants' movement patterns. We created detailed maps of herbaceous and woody cover, density, and biomass based on satellite imagery. We predict that movement patterns would reveal the relative preference for each vegetation type.

(2) How does elephant resource preference, as indicated by the movement decisions of individuals, vary temporally?

We hypothesize that the relationship between the landscape and emerging movement patterns will vary with both time and temporal scale of analysis, from diurnal to annual scales. The movement response of individuals should reveal temporal segregation in resource use. On a diurnal scale, hourly variations in speed of movement and in resource preference should reflect behaviors leading to that preference (e.g., feeding on different vegetation types, drinking, directional walk, resting). On a seasonal scale, the movement response of individuals to underlying landscape variables should reflect the availability and ecological importance of the resource in each season.

(3) What is the temporal scale of resource availability elephants respond to?

We hypothesized that the strongest response would be to current vegetation conditions, while preference will decline with information on vegetation productivity, in previously visited locations, integrated over the past year, or over the long-term of the whole research period. To that end, we integrated various lengths of time series of vegetation indices, derived from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery, and examined how elephants move in response to each temporal time span.

METHODS

Study area

Etosha National Park (Etosha) is a 22,270 km^2 reserve located in north-central Namibia (19° S, 16° E; Appendix S1: Fig. S1). It is a semiarid savanna with an east-west rainfall gradient of 200–450 mm/yr. There are three main seasons in Etosha: the cold-dry (May to August), hot-dry (September to December), and the hot-wet (January to April; Du Plessis 1999). Rains start in November and periodically continue through April; peak rainfall occurs in January and February (Turner and Getz 2010). Etosha is primarily flat, transitioning to hillier terrain in its far west. The main vegetation types in the reserve are grasslands; steppe, dominated by dwarf shrubs, primarily *Leucosphaera baenesii* and *Monechma genistifolium*; shrubland, dominated by *Catophractes alexandri* and *Acacia* spp., mainly *Acacia nebrownii*; Mopane (*Colophospermum mopane*) tree savanna; and mixed trees savanna dominated by *Commiphora* spp., *Combretum*, *Grewia*, *Terminalia prunioides*, *Terminalia sericea*, and *Ziziphus mucronata* (Le Roux et al. 1988, Du Plessis 1999). Etosha has been fully fenced since the early 1970s. Fifteen artificial waterholes provide water to wildlife year-round. The size of African elephant population in Etosha was estimated to be around 2,600 in the 2005 aerial census (de Beer et al. 2006, Turner et al. 2013).

Landscape information

We mapped herbaceous and woody vegetation in Etosha with a novel methodology for modeling the relationship between extensive field sampling and Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery. Based on these models, we created detailed maps of the cover, density, and biomass of woody and herbaceous vegetation in Etosha, as described in Tsalyuk et al. (2017). In short, we measured the density, cover, and biomass of the main vegetation types in Etosha: grasses, shrubs, and trees, in 348 sampling points across Etosha, during the dry and wet season. We created partial least square regression (PLSR) models for time series data of four MODIS-derived vegetation indices (VIs) to predict each field measurement (cover, density, and biomass) for each of the main vegetation types (trees, shrubs, and grasses). The four VIs we used were normalized difference vegetation index (NDVI), enhanced vegetation index (EVI), leaf area index (LAI), and fraction of photosynthetically active radiation (FPAR; Knyazikhin et al. 1999) NDVI may be a poor predictor of vegetation structure of sparse dry savannas if based on single date or short-term composite imagery alone (Tsalyuk et al. 2015). By using multiannual time series of four VIs we were able to create robust prediction models for each vegetation type with high variance explained and low error (Tsalyuk et al. 2017). For each vegetation variable, we selected the VI-based model that resulted in the highest percentage of variance explained (equivalent to R^2) and the lowest leave-one-out cross-validation root mean squared error of prediction (RMSEP; Mevik and Cederkvist 2004, Darvishzadeh et al. 2008). NDVI was the best predictor of tree density ($R^2 = 0.79$, relative root mean square error [rRMSE], or percent error = 1.9%), tree cover ($R^2 = 0.78$, rRMSE = 0.3%), and tree biomass ($R^2 = 0.75$, rRMSE = 0.6%). Selected model for measurement of shrub density was based on LAI ($R^2 = 0.81$, rRMSE = 0.3%); for shrub cover on EVI ($R^2 = 0.76$, rRMSE = 0.8%); and for shrub biomass on NDVI ($R^2 = 0.76$, rRMSE = 0.6%). Best predictive models for grass cover ($R^2 = 0.82$, rRMSE = 44.1%) and grass biomass ($R^2 = 0.91$, rRMSE = 48.1%) were based on FPAR. For more details on the creation and selection of vegetation models, see Tsalyuk et al. (2017).

In addition to the above vegetation measurements, we used MODIS-derived vegetation indices directly, as a measure of temporal variability in vegetation primary productivity. NDVI is a measure of vegetation productivity and green biomass (Pettorelli 2013). FPAR measures the proportion of sun radiation received by the plant, out of the total available radiation in the photosynthetically active wavelengths of the spectrum 400–700 nm (Knyazikhin et al. 1999). FPAR is a functional measure of vegetation photosynthetic activity. Since photosynthetic activity continues, to some degree, in dry vegetation, FPAR is related to both green and dry vegetation biomass (Tsalyuk et al. 2015). Although FPAR and NDVI are correlated, we added FPAR as an explanatory variable of elephant movement because FPAR is a better predictor than NDVI of dry forage and herbaceous biomass (Machwitz et al. 2015, Tsalyuk et al. 2015). We acquired all MODIS data version V006 available for the years 2000–2014 from the online Data Pool, courtesy of the NASA Land Processes Distributed Active Archive Center (LP DAAC 2000–2014). MODIS NDVI is provided at a 250 × 250 m resolution, as a 16-d composite; FPAR is provided at a 500 × 500 m resolution as an 8-d average. We resampled FPAR to match the 250 × 250 m resolution. For each pixel, we calculated multiannual mean and variance of NDVI or FPAR for the years 2007–2014. This period includes the years GPS collars were deployed (2008–2014); we added one year of vegetation productivity data prior to the start of the study (2007), assuming it will have direct effect on the vegetation condition at the beginning of the study (Tsalyuk et al. 2017). Additionally, for each individual elephant, we calculated the 10-yr average of NDVI or FPAR, prior to the date of the individual's last recorded movement point.

We calculated minimum Euclidean distance to roads, water sources, and the fence, based on GIS layers for Etosha provided by the Etosha Ecological Institute (EEI), using the distance function (package raster, R 3.3) (Hijmans 2017; R Core Team 2018). We assumed the fence would only influence elephant movement relatively close to it (Vanak et al. 2010). Therefore, we included distance from the fence as a covariate in our models only within 10 km from the fence; model for locations at distance farther than 10 km did not include the fence variable.

Data rasters for all variables were created using resolution of 250 × 250 m^2 to match MODIS imagery resolution and were scaled to have a mean of 0 and standard deviation of 1.

We estimated the effect of tourist car density on elephants by calculating average monthly tourist travel in Etosha, using the number of cars entering daily at the main entrance of Etosha, Anderson gate. Rainfall data were obtained from 168 rain gauges distributed around Etosha. For each rain gauge, we averaged rainfall data for 2009–2010. We used the kriging function (Spatial Analyst Tools, ArcGIS 10.2; ESRI 2011) extrapolate these point data to the entire reserve.

Elephant movement data

We fitted 15 elephants with GPS/GSM platform collars (Africa Wildlife Tracking, Pretoria, South Africa), eight cows and seven bulls, all from different groups. Collaring was performed in the central part of Etosha, around Okaukuejo station (15°55′20.156″ E 19°10′49.736″ S). Darting and collaring procedures were performed by veterinarians from the Namibian Ministry of Environment and Tourism in compliance with the University of California Berkeley animal care and use protocol (#R217-0511B). Elephants were collared during two periods, October 2008 and July 2009; data were collected for 2.2 months to 4.6 yr (October 2008–March 2014) (Appendix S1: Fig. S2). Location information was recorded in time intervals alternating between 1 min and 19 min. GPS collar accuracy was ±3 m, as was confirmed in the field. This produced a data set of 1.37 million GPS fixes, with an average of 114,246 data points for each calendar month, and 450,794 points for each of the three main seasons. For individual elephants, the number of GPS fixes ranged from 11,513 to 210,493, with a median value of 89,326 points. The data used in this study are from the Movebank Data Repository under the study name "*Loxodonta africana* Etosha National Park" (Getz et al. 2018; see *Data Availability*).

Our relatively small sample size of 15 individuals may limit the generality of our conclusions. However, the strength of our data set lies in the combination of high temporal resolution of movement data (1 min) with high spatial and thematic landscape information. Our data set spans six years with repeated seasons for most individuals (Appendix S1: Fig. S2). Moreover, since each elephant represents a different group, and group members have correlated movement patterns, it enhances the representability of our results (Wittemyer et al. 2008).

Movement analysis

We first analyzed diurnal and seasonal variation in movement patterns (speed, turning angle, directedness). We then related temporal variation in movement patterns to changing landscape variables and to variations in vegetation primary productivity. To understand temporal variation and the effect of temporal scales of analysis on movement patterns, we performed analyses at increasing time scales: 1/60-, 1/3-, 1-, 3-, 6-, 12-, and 24-h intervals between consecutive GPS fixes. For the analysis at the 1/60-h interval, we subsampled the movement record to take only the 1-min intervals. For each acquired location, we calculated the distance to the next fix (step length), movement speed (km/h), turning angle (degrees), and relative turning angle (radians); the latter two were calculated at intervals of 20 min and above.

We measured the effect of temporal scale of analysis on movement directedness (i.e., more or less diffusive) using the parameter p in the equation $D_T = D_1 T^p$, where D_T is the average distance traveled in intervals T minutes apart, D_1 is the average distance an individual elephants travels in 1-min intervals (Appendix S2: Table S1). Hence

$$p = \log(D_\mathrm{T}/D_1)/\log(T) \tag{1}$$

We calculated p for each individual and for each time interval between 20 min and 24 h, in 1-h steps. Values of p around 1 correspond to directed movement, with $p > 1$ implying directed movement at greater than average speeds (which typically only occur over comparatively short intervals of time). Values $0.5 \leq p \leq 1$ correspond to more diffusive movement as p tends to 0.5, while $p < 0.5$ implies that lingering periods (e.g., resting or foraging around one location) begin to predominate (Getz and Saltz 2008).

We examined the diurnal temporal variation in each elephant's speed across time of day and across months, as well as for the whole population (data pooled from 15 individuals). We analyzed diurnal variation in speed during eight periods of the day, spanning three hours around sunrise (05:00–08:00), noon (11:00–14:00), sunset (17:00–20:00), and night (23:00–02:00), and the time intervals in between. We analyzed seasonal variation in movement speed in each of the main seasons in Etosha: the cold-dry season (May to August), hot-dry season (September to December), and the hot-wet season (January to April; Turner et al. 2013).

We used step selection function (SSF) to analyze elephants' movement response to landscape variables. The SSF analyzes individual movement characteristics in the context of local landscape. SSF defines the domain of availability of a resource, in terms of the resources available to the animal in its immediate surroundings, at each point in time (Forester et al. 2009). For each actual step, we created $k = 20$ case-control steps (Forester et al. 2009). The control steps were created using step size and turning angle drawing from the individual-specific distributions of these two quantities. This analysis was repeated using the distributions of the population (i.e., movement data aggregated across all 15 individuals). Each of the actual steps and the 20 case-control steps identified a particular 250×250 m^2 pixel, from which we extracted the underlying landscape variables. We repeated SSF analysis twice, at two temporal scales: 20-min intervals or one-hour between consecutive steps (GPS fixes).

Elephants' preference for landscape variables was calculated using conditional logistic regression, which maximizes the likelihood of the chosen steps. The probability of the animal to choose the actual step, compared to the 20 case-control steps, is a function of the landscape variables underlying these steps; the step size, and absolute relative turning angle were included in the model as well (Forester et al. 2009). We used the clogit function from the survival package in R to estimate model coefficients (Therneau 2015). The magnitude of the coefficients indicates the relative importance of each landscape variable in determining elephants' movement decisions, given that explanatory variables were standardized. Statistical significance of the conditional logistic regression results was evaluated based on the P value on each resulting coefficient, indicating whether it was significantly different than zero. Standard error around each coefficient estimate and 95% confidence intervals were calculated to compare the effect of each variable on movement relative to other variables. To ease interpretation of the figures, sign of coefficients on distance variables (water points, roads, and the fence) were reversed by multiplying values by -1, such that a positive coefficient value implies preference for the variable in question, while negative coefficients imply avoidance.

We created a multivariate model that included all the uncorrelated landscape variables. To reduce the potential effect of collinearity in the predictor variables, we calculated a pixel-based Pearson correlation coefficient for every pair of landscape predictor variables. We included only variables that had $r < 0.7$ (Appendix S2: Table S2; Dormann et al. 2013). As a result, biomass (the net dry amount of each vegetation type) was used in the full model: grass biomass, shrub biomass, and tree biomass, together with long-term (multiannual) mean and variance of NDVI, and distance to water sources, roads, and the fence (within 10 km from the fence). FPAR and NDVI are correlated but provide complementary information on landscape state, with FPAR being a better predictor than NDVI of dry forage and herbaceous biomass. Therefore, we created a separate model using only multiannual mean and variance of FPAR, and without biomass variables.

Temporal variation in resource selection

We examined the effect of landscape on elephants' movement across time. To understand the influence of time of day on resource selection, we created a model that included interaction terms between landscape variables and, following Forester et al. (2009), four harmonics of time of day (time recorded in decimal hours). We examined the effect of season on resource selection by creating a model that included month as a cofactor.

All SSF models examining temporal variation were performed for 1-h intervals between consecutive fixes.

Temporal scale of information integration of resource availability

In our SSF studies, we evaluated how elephants integrate spatial information over time by comparing elephant movement responses to the state of the resources at three temporal scales, as detailed below: (1) as close as possible to contemporaneous, (2) annual average, and (3) long-term average (10 yr). We examined vegetation primary productivity measured by MODIS-derived NDVI or FPAR as the resource we considered for these analyses.

To ensure that the elephants had prior information on each location, we calculated for each raster cell, and for each individual, how many times and on how many separate dates each individual visited that cell, using the resolution of the landscape data of 250 × 250 m. Only locations previously visited by a given elephant were used for the SSF conditional logistic regression for this part of the analysis. Unfortunately, we could not account for the fact that these data did not provide information on use of the area prior to the study period, nor could we account for information about resources transmitted socially.

To understand the seasonal and multiannual variability of productivity in Etosha, we constructed a time series plot of NDVI/FPAR for 2007–2014. Next, we created SSF conditional logistic regression models as a function of NDVI or FPAR at three temporal scales, calculated separately for each individual. (1) Closest date: MODIS NDVI/FPAR integrated for 16- or 8-d interval, respectively, in the time interval immediately *prior* to the elephant's moving in that pixel, as recorded by each GPS fix. This scale indicated the resource availability, as perceived by the elephants immediately at the time of movement. (2) Annual average: 12-month mean of NDVI/FPAR prior to the elephants' movement through the location. This scale indicates changes in resource availability on an intermediate temporal scale. (3) Long-term average: NDVI/FPAR multiannual mean for 10-yr, prior to the date of the movement point of each individual. This scale indicates the long-term information elephants have about resource distribution on a large spatial and temporal scale. We created a SSF model for each temporal scale, separately.

To understand the seasonal variation in response to temporal scales of productivity availability, we created SSF models using month as a covariate, for each of the three temporal scales separately. We compare monthly variation in the SSF model coefficients (± SE) to examine the significance of the differences among each of the three temporal scales across seasons.

RESULTS

Effect of temporal scale on movement metrics

Our results indicate that temporal scale of analysis has a strong effect on the statistics of resulting movement metrics statistics. On average, elephants move slowly with high directional persistence. The average step length (linear displacement from origin position) when analyzing 1-min intervals between consecutive fixes is 32 m. Average step length was 200 m when analyzing 20-min intervals between fixes, and 554 m for 1-h time intervals, corresponding to a speed of 0.55 km/h (Appendix S1: Fig. S3, Appendix S2: Table S1). The turning angle had similar probability in all directions relative to the north, but there was some tendency toward east-west movement (90° or 270°) in the 1-min time interval analysis (Appendix S1: Fig. S3A). Relative turning angle was distributed around zero radians, with no bias in turning direction (i.e., clockwise vs. counterclockwise movements), which suggests a tendency for directional persistence.

There was marked variation among individuals in the pattern of movement directedness as a function of time scale of analysis between consecutive fixes (Fig. 1). Directness patterns diverged into two main strategies. For some individuals, mainly females, short-term scale encampment (i.e., remaining within a local area) decreased and movement became more directed as time increased over the first 3 h (i.e., values of p, given by Eq. 1, increased from close to zero to around 0.7), but leveled off as time increased beyond 3 h (Fig. 1). Other individuals, mostly young adults and few adult males, had hyper-directed movement ($p \gg 1$; i.e., the further the animal went the faster it moved on average) for smaller time intervals that approached $p = 1$ when the interval approached 24 h.

Temporal variations in movement speed

Our results demonstrated diurnal and seasonal variation in African elephant movement speed and direction.

Movement speed varied throughout the day; the fastest movement was in the afternoon (16:00–17:00, Fig. 2A, B). Average speed fluctuated throughout the year: speed was slower (0.52 km/h) in the cold-dry season (July to September) and fastest (0.59 km/h) in the wet season (March to May), and around November (Fig. 2C, D).

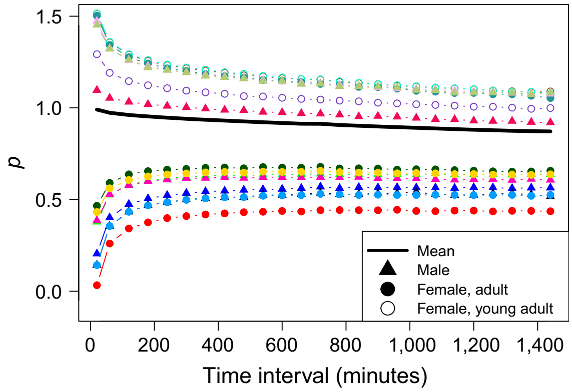

FIG. 1. Movement directness as measured by parameter p fitted to Eq. 1 ($p = 0.5$ and $p = 1$, respectively, correspond to diffusion and straight-line movement). Each point is the mean p of each elephant at each time interval between consecutive GPS fixes. The black line represents the mean of all 15 individuals. Values of p around 1.5 correspond to hyper-directedness (i.e., 50% higher than average speeds in a particular direction) and values of $p < 0.5$ correspond to encampment (resting or foraging in a local patch).

Relative importance of landscape variables

Anthropogenic landscape features in Etosha affect elephant movement greatly: elephants tended to move close to artificial water and close to roads (Fig. 3). Artificial water sources (i.e., bore holes) had the strongest influence on elephant movement. Preference to walk close to roads was associated with the quality of road; paved roads were stronger attractors than lower quality roads, such as track roads or firebreaks (Appendix S1: Fig. S4). Elephants walked closer to the fence when walking within 10 km from it (Fig. 3). Elephants preferred high mean NDVI, indicating selection for higher vegetation productivity and greenness. Notably, high temporal variance of NDVI was preferred. Elephants preferred higher FPAR (Appendix S1: Fig. S5) and high grass biomass, but lower tree biomass values (Fig. 3). Coefficient of selection for shrub biomass was not significant (Fig. 3).

Comparing SSF models constructed for each individual with a SSF model constructed for the population as a whole (15 elephants) indicated little difference in the resulting coefficients. However, lower variation in the

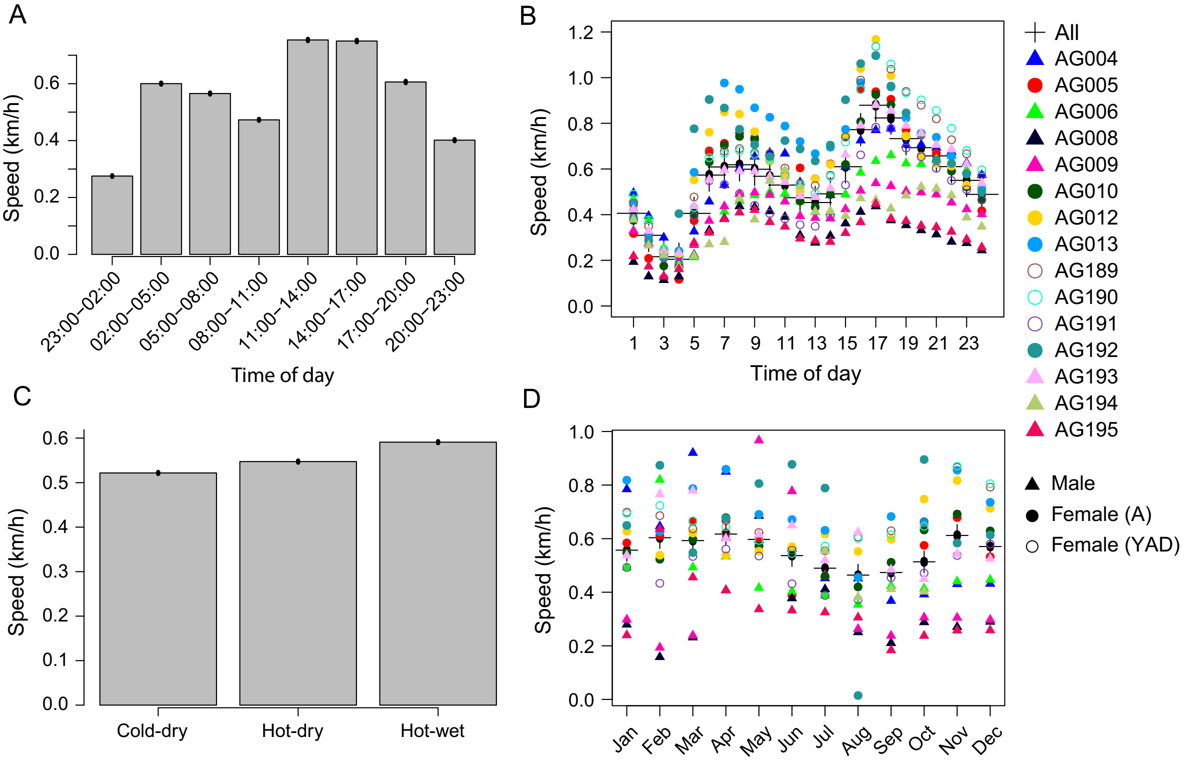

FIG. 2. Temporal variation in elephants' movement speed (km/h) ±95% confidence intervals. Speed was calculated for 1-h time intervals between consecutive steps, for the whole population (15 elephants) and for each individual at two time scales: (A) diurnal variation in speed of the population and (B) diurnal variation among individuals. The average speed of the population and of each individual is marked. (C) Seasonal variation in speed of the population. (D) Monthly variation among individuals. A, adult; YAD, young adult.

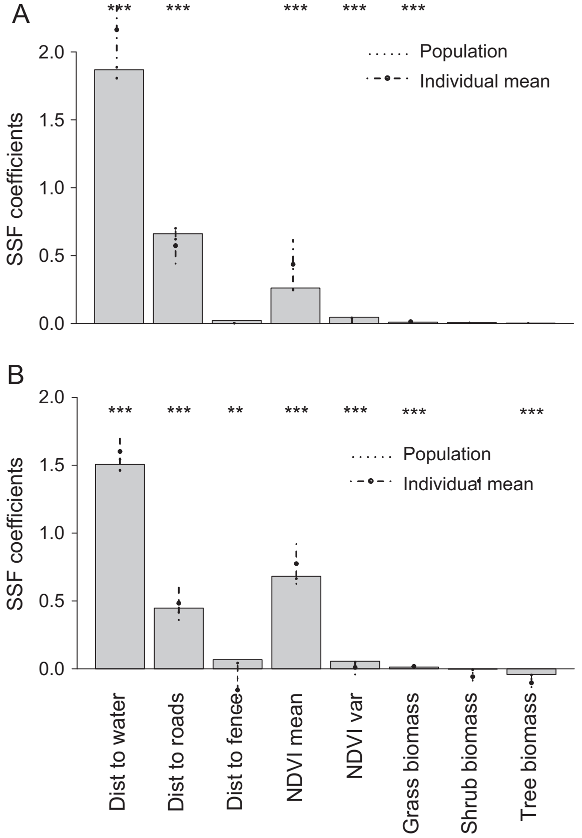

FIG. 3. Relative importance of landscape variables in elephants' movement patterns as measured by coefficients (mean ± SE) on step selection function (SSF). Coefficients on distance variables were reversed, such that positive values mean preference to be *closer* to the feature. SSF analysis was performed for the whole population (dotted line) or for each individual separately and then the coefficients of all individuals were averaged (dot-dashed line). Analysis for step intervals between consecutive fixes of (A) 20-min and (B) 60-min intervals. Asterisks above columns denote significance of coefficient values: ** $P < 0.01$; *** $P < 0.001$. Dist, Distance; NDVI, normalized difference vegetation index; var, multiannual variance.

coefficients (larger standard error) was associated with the population level model.

The temporal resolution of analysis (1-h vs. 20-min intervals between consecutive fixes) had little effect on the relative importance of landscape variables, as measured by SSF coefficients (Fig. 3). NDVI had larger coefficients than distance to roads in the 1-h resolution analysis. Additionally, preferences to walk closer to the fence and farther from high tree biomass were significant only in the 1-h resolution analysis (Fig. 3).

Temporal variation in resource selection

Elephants' preference for landscape variables varied throughout the day and changed with season.

Diurnal temporal variation had a marked effect on the strength and, in some cases, the direction, of the response to landscape variables (Fig. 4). Preference for long-term (multiannual) average NDVI was highest around midday (10:00–12:00; Fig. 4A). Preference for grass biomass peaked around early morning (05:00) and in the afternoon (17:00–19:00; Fig. 4B). High tree biomass was avoided most of the day; this avoidance was most pronounced at night but diminished around noon (Fig. 4B). Elephants preferred to be close to surface water mostly in the evening (around 19:00) and at night and walked away from water around noon (Fig. 4C). Similarly, elephants walked close to roads at evening and night, but avoid roads around midday (Fig. 4D).

There was pronounced seasonal variation in movement response to landscape variables (Fig. 5, Table 1). High NDVI was preferred year-round, but this preference was strongest in the cold-dry season (June to August). Preference for high temporal variance of NDVI was highest in the rainy months (December to March), but low in the cold-dry season (June to August) (Fig. 5A). The response to NDVI temporal variance was inversely correlated to the response to NDVI mean ($\beta = -1.89$, $R^2 = 0.39$, $P = 0.016$; Fig. 5A). Elephants' responses to FPAR mean and variance were also opposite to each other ($\beta = -1.02$, $R^2 = 0.67$, $P < 0.001$; Fig. 5B). Elephants preferred higher FPAR mean but avoided FPAR variance during the dry months; high FPAR was also avoided in the wet season, around February (Fig. 5B).

Different vegetation types were utilized at different times of the year. Grass biomass was most strongly preferred in the hot-dry months, but avoided in the cold season (Fig. 5C). Conversely, shrub biomass was most preferred in May and in October but was avoided in February and March, when rainfall was relatively high (Fig. 5D). High tree biomass was avoided most of the year; this avoidance was strongest in the rainy season (Fig. 5E). Elephants walked closer to the fence in the dry months (July to October) but avoided it in the rainy months (February) (Fig. 5F).

While elephants preferred to be close to water year-round, this preference was inversely related to the average monthly rainfall and was strongest in the hot-dry months (Fig. 5G). There was a lag between decline in monthly rainfall and the subsequent increased preference for surface water in the following months (Fig. 5G).

Preference to walk closer to roads persisted year-round; this preference was strongest in the dry months (August and October; Fig. 5H). There was a positive relationship between preference for roads and the number of tourists' vehicles entering Etosha each month (Fig. 5H).

Temporal scale of response to resource availability

Vegetation productivity, as measured by MODIS-derived vegetation indices (VIs), NDVI, or FPAR, showed a unimodal annual cycle in Etosha (Fig. 6). This cycle represents availability of forage resources and

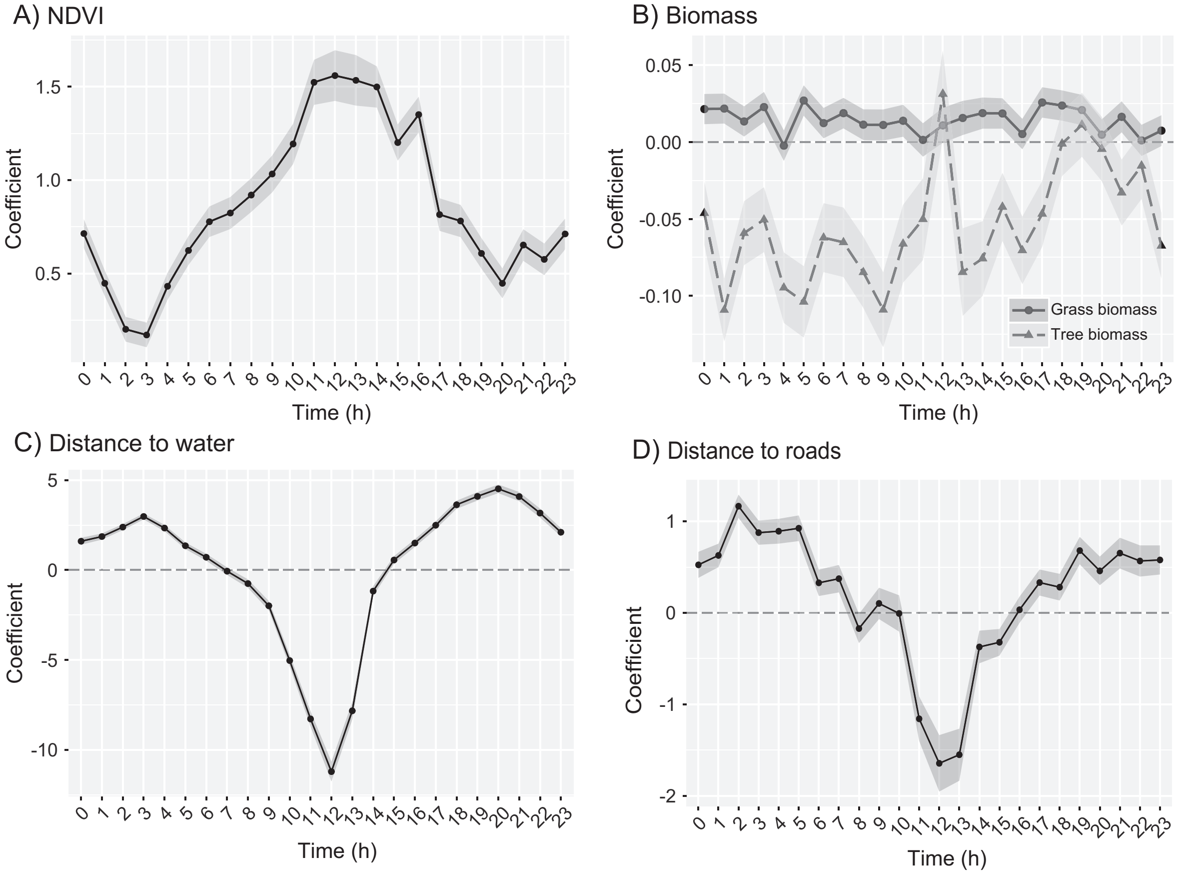

FIG. 4. Diurnal variation in preference of landscape variables as measured by coefficients (mean ± SE, shown by shading) on step selection function (SSF): (A) NDVI (multiannual mean), (B) biomass of grass and trees, (C) distance to water, (D) distance to roads. Coefficients on distance variables were reversed, such that positive values mean preference to be closer to the feature.

determines the relative abundance of the resources throughout the year. Minimum values of NDVI/FPAR occurred around 6 September, while the maximum occurred around 10 March and 29 March, for NDVI and FPAR, respectively (Fig. 6).

We examined elephants' selection of NDVI/FPAR in previously visited locations in three temporal scales: NDVI at the time of the elephant movement in each pixel (closest date), average of one year prior to the elephant's arrival to the pixel (annual average), and multiannual NDVI/FPAR average over the whole research period (10-yr, long-term average). Preference for multiannual NDVI/FPAR was significantly higher than preference for annual mean NDVI/FPAR; preference for annual mean was significantly higher than NDVI/FPAR at the time of elephant's movement, as indicated by non-overlapping confidence intervals on the coefficients (Table 2).

Elephants' seasonal response to NDVI in locations the individuals had previously visited, showed similar patterns for all three temporal scales of NDVI/FPAR integration (Fig. 7); this preference increased in the dry season and peaked in August. Seasonal preference for long-term NDVI was significantly higher than preference for annual average NDVI most of the year, but this difference was not significant in April to July. Seasonal preference for annual average NDVI was, in turn, higher than preference for NDVI at time of movement. The differences among the response to temporal scales of NDVI integration were especially prominent in the hot-dry season (August to December; Fig. 7A).

The preference for FPAR was highest in July and October. The response to long-term FPAR average was stronger than response to the annual average, which, in turn, was stronger than the closest date FPAR values (Table 2). These differences in the seasonal response to the three temporal scales were most significant in the dry months, July to October (Fig. 7B).

DISCUSSION

Ungulates need to adjust their spatial distribution to temporally varying resources in order to survive (Fryxell et al. 2005). In this paper, we demonstrate the importance of diurnal and seasonal temporal variations in African elephant movement responses to landscape variables, by combining high temporal resolution telemetry

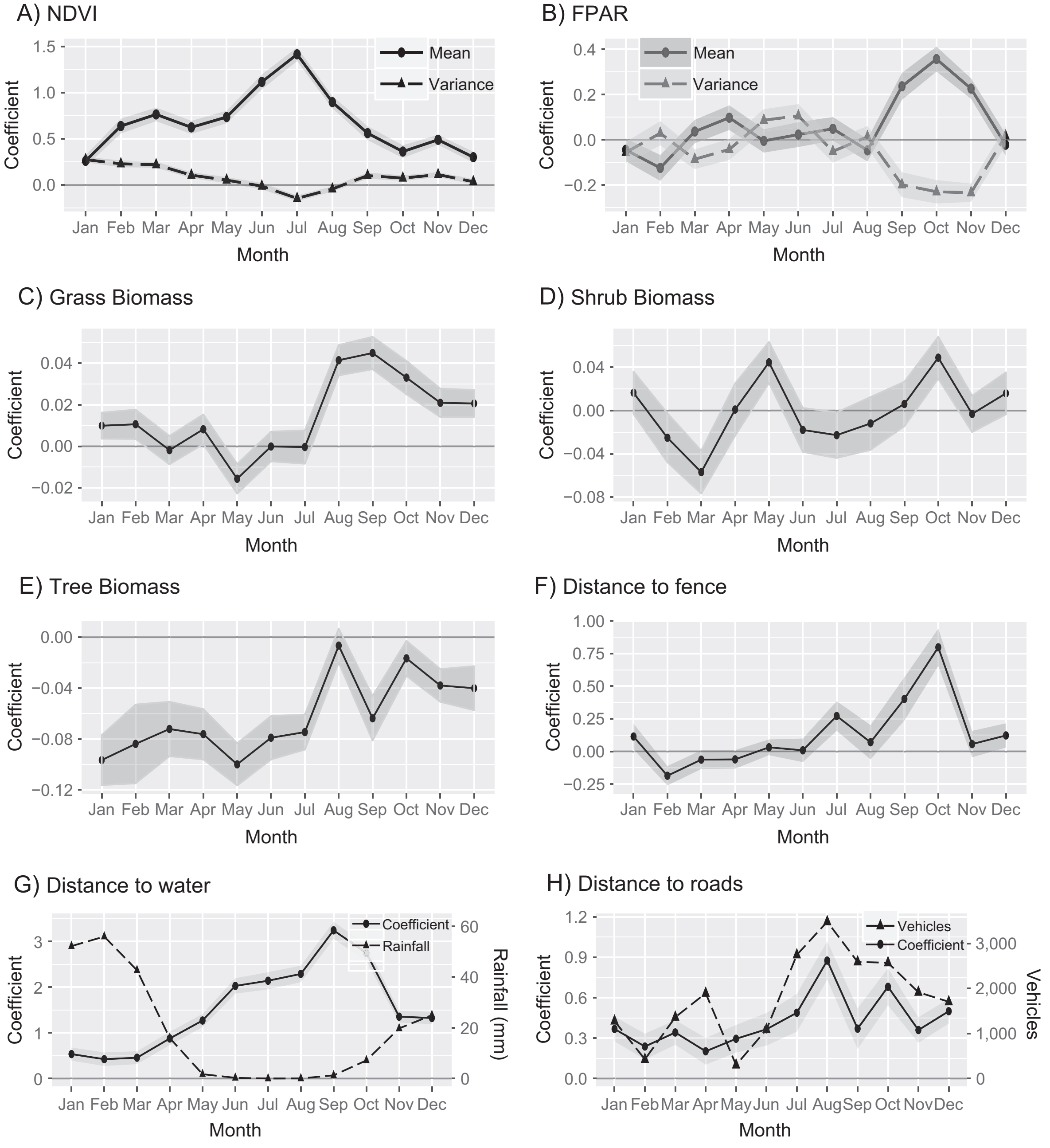

FIG. 5. Monthly variation in preference of landscape variables as measured by coefficients (mean ± SE) on step selection function (SSF): (A) mean and variance of NDVI, (B) mean and variance of fraction of photosynthetically active radiation (FPAR), (C) grass biomass, (D) shrub biomass, (E) tree biomass, (F) distance to the reserve's fence, (G) distance to water (dashed line denotes mean monthly rainfall), and (H) distance to roads (dashed line denotes mean number of tourist vehicles entering the reserve). Coefficients on distance variables were reversed, such that positive values mean preference to be closer to the feature.

information with high thematic and temporal resolution satellite imagery.

Temporal variation in movement metrics

An important insight obtained from this research is that temporal scale of analysis can significantly affect conclusions about movement patterns and resource selection. Temporal scale is expected to have a strong effect on movement metrics statistics (Codling and Hill 2005, Getz and Saltz 2008, Plank and Codling 2009). Here, we show that increasing the scale of analysis, from 20-min to 24-h intervals between consecutive fixes, had only a mild effect on the statistics of most movement metrics (speed, angle,

Table 1. Resource preference of African elephants in Etosha National Park as summarized from coefficients on step selection function (SSF).

	Hot-wet months				Cold-dry months				Hot-dry months			
Resource	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Grass	ns	ns	ns	ns	–	ns	ns	++	++	+	+	+
Shrubs	ns	ns	–	ns	+	ns	ns	ns	ns	+	ns	ns
Trees	—	—	–	–	—	–	–	ns	–	ns	–	–
FPAR	ns	–	ns	ns	ns	ns	ns	ns	+	++	+	ns
NDVI	+	+	++	+	++	+++	+++	++	+	+	+	+

Notes: + preference; +++ strong preference; – avoidance; — strong avoidance; ns, not significant. FPAR, fraction of photosynthetically active radiation; NDVI, normalized difference vegetation index.

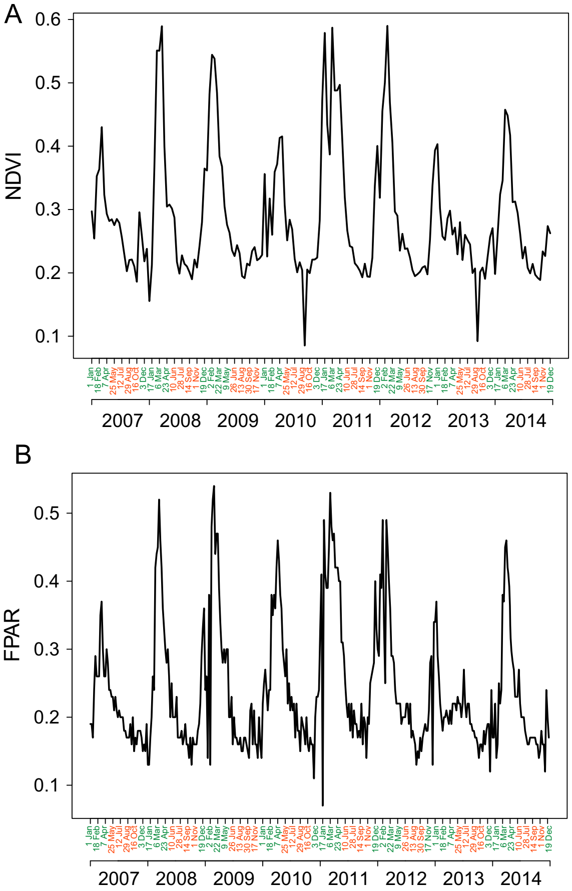

Fig. 6. Time series of MODIS-based vegetation indices in Etosha National Park for 2007–2014: (A) normalized difference vegetation index (NDVI) and (B) fraction of photosynthetically active radiation (FPAR). Orange and green dates depict dry and wet seasons, respectively.

turning angle; Appendix S1: Fig. S3), however, movement directedness varied markedly (Fig. 1). Variability among individuals in directedness as function of sampling rate indicates that there is a marked inter-individual variability in the foraging strategies and, consequently, in the diurnal movement periodicity among elephant individuals (Wittemyer et al. 2008). There was divergence into two movement strategies; young adults and some males exhibited hyper-directed movement in shorter time intervals. This may be explained by exploratory movement of young adults, moving farther to examine new locations and resources; subordinate individuals walk longer distances and demonstrate less repeatability in their movement due to interference competition (Wittemyer et al. 2008, Boettiger et al. 2011). We also note that the emergence of discrete movement strategies, with an absence of intermediates is related to the evolution of behavioral guilds, where each strategy is a member of an "ideal free distribution" with regard to maximizing fitness, so that intermediate strategies are less fit (Getz et al. 2015, 2016). Discrete movement behavioral types have also been observed in other species (Abrahms et al. 2017), and in other evolutionarily driven behavioral contexts, such as cannibalism (Moleón et al. 2017).

Sampling rate of movement locations may affect the resulting resource selection. In this research, there were small differences in the relative importance of landscape variable when comparing SSF performed in 20-min or 60-min time intervals between fixes (Fig. 3). Coefficients associated with distance to the fence and shrub biomass became significant only when analyzing data at a 60-min scale. The sensitivity of resource selection to sampling rate can result from statistical or ecological processes. Reduced sampling rate may increase the precision of movement patterns (Codling and Hill 2005, Plank and Codling 2011). Furthermore, many movement analysis methods require that the movement sampling intervals are close to the timescale characterizing the movement behavior, an assumption that is not frequently met. Additionally, animals use different resources at different temporal scales and during different behavioral modes, such as intrapatch, interpatch, or migratory-type movements. Applying resources selection function to discrete movement modes can produce results that are less sensitive to sampling rates (Johnson et al. 2002, Fleming et al. 2014).

Relative importance of landscape variables in determining elephant movement

We found that anthropogenic landscape features, namely artificial water sources, roads, and fences, had the

TABLE 2. Coefficients and standard errors on step selection functions (SSF) fitted with conditional logistic regression on MODIS-derived vegetation indices (VI) in previously visited locations: normalized difference vegetation index (NDVI) and fraction of photosynthetically active radiation (FPAR).

Time scale	Coefficient	SE	*z*	*P*
NDVI				
Closest date	0.25	0.01	23.63	<0.001
Annual average	0.38	0.02	22.01	<0.001
Long-term average	0.47	0.02	25.92	<0.001
FPAR				
Closest date	0.07	0.01	11.04	<0.001
Annual average	0.11	0.01	10.37	<0.001
Long-term average	0.17	0.01	13.57	<0.001

Notes: VI data were integrated over three time scales: (1) closest date is VI 16-d composite value immediately prior to the date of the elephant's movement at the point; (2) annual average is average VI for 12 months prior to the elephant's movement at the point; and (3) long-term average is multiannual average VI (10 yr).

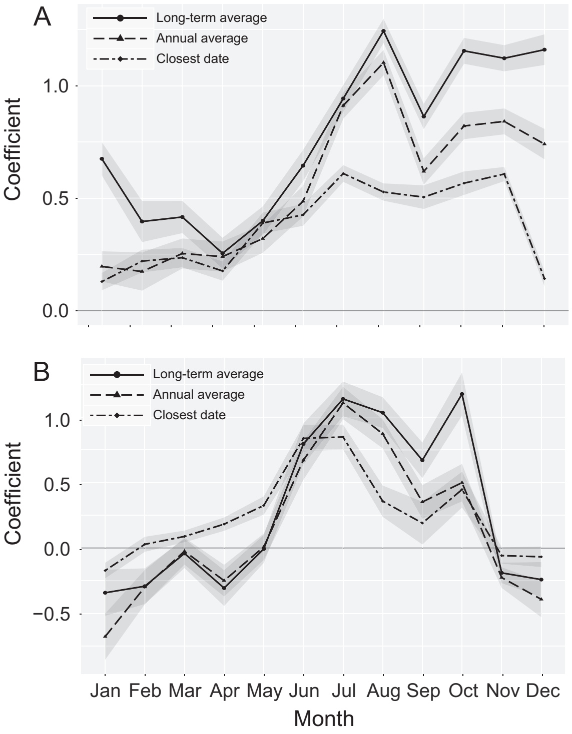

FIG. 7. Temporal variation in movement response to productivity at previously visited locations as measured by two MODIS-based vegetation indices: (A) normalized difference vegetation index (NDVI) and (B) fraction of photosynthetically active radiation (FPAR). Three time scales are compared: the value measured immediately prior to time of the elephant's movement ("closest date"), annual average of the year prior to the elephant's movement ("annual average"), and multiannual average of 10 years prior to the elephant's movement ("long-term average"). Values show SSF coefficients. Dashed lines denote ±95% pointwise confidence intervals.

strongest influence on elephant movement (Fig. 3). Elephants' strong preference to be close to water is expected in the semiarid environment of Etosha. Elephants depend on surface water and drink daily (Owen-Smith 1996).

Somewhat less expected was the elephants' preference to walk close to roads. This preference suggests that elephants use roads as a locomotion surface to reduce energy expenditure. Previous research showed that ungulates use roads in protected areas as low resistance corridors. This assumption is strengthened since elephants had stronger selection for better quality roads (Appendix S1: Fig. S4). Additionally, artificial waterholes in Etosha are located along the roads, making roads the fastest direct route between watering points. Stronger preference for roads in the dry season (see below, Fig. 5H) supports this explanation: roads are highly preferred in the dry season, when the quality of the roads is in its best and when the need to move furthest between water and vegetation resources is the highest. Additionally, mammals may prefer roads because of higher availability of greener vegetation in ditches alongside roads, or because they use tourist vehicles as shields from predators (Trombulak and Frissell 2000, Berger 2007).

Mean NDVI had the strongest influence on elephant movement, of any variables tested (Fig. 3). NDVI is a measure of vegetation productivity and green biomass (Pettorelli et al. 2005). As megaherbivores, elephants consume 50–200 kg of food each day and therefore require areas with large amounts of forage (Sukumar 2003). Elephants in Etosha also preferred areas with high FPAR (Appendix S1: Fig. S5). Unlike NDVI, which mainly quantifies green vegetation biomass, FPAR measures the photosynthetic capacity of vegetation, which continues, to some degree, in dry vegetation as well (Butterfield and Malmstrom 2009, Tsalyuk et al. 2015). Therefore, FPAR measures both green and dry biomass, and is strongly correlated with herbaceous vegetation (Tsalyuk et al. 2017).

Elephants are mixed feeders that consume both herbaceous and woody vegetation. According to our satellite-based vegetation models, NDVI was the best predictor of tree biomass while FPAR was the best predictor of predictor of grass biomass (Tsalyuk et al. 2017). Selection of areas with either high NDVI or high FPAR indicates elephants' mixed utilization of both herbaceous and woody habitats. Moreover, our results imply that elephants utilize both fresh (green) and dry patches of vegetation (Fig. 3; Appendix S1: Fig. S5). Elephants are able to select nutrient-rich plants at a variety of scales, and therefore can extract nutritious forage within drier patches (Pretorius et al. 2011). Preference for areas with high FPAR demonstrates the importance of using this vegetation index, in addition to NDVI, as a proxy for vegetation availability to wildlife in semiarid environments.

Notably, elephants in Etosha prefer areas with high grass biomass, but low tree biomass (Fig. 3). Preference of grasslands may be driven by easier movement through open landscapes or perceived safety for better detection of predators (Loarie et al. 2009*a*,*b*). Previous research indicated different conclusions regarding elephants' preference of woody vs. grass habitats. For example, in Kenya elephants preferred high tree density (Riginos and Grace 2008), while in Kruger National Park female elephants preferred areas with high herbaceous biomass but lower tree cover (de Knegt et al. 2011). A possible explanation for stronger preference of high grass biomass in Etosha can be that elephants in Etosha rely more on grazing than on browsing. Elephants feed on higher percentage of herbaceous vegetation in more arid environments (Codron et al. 2006, 2012). Grass diet may be advantageous since nutrient concentrations in grasses in drier areas are higher than in wetter areas (Hopcraft et al. 2010). Moreover, large areas in Etosha are dominated by *Colophospermum mopane* trees, which might not supply the adequate nitrogen and phosphorus content needed for elephants (Pretorius et al. 2011, Turner et al. 2013). Indeed, Elephants in *mopane*-dominated regions within Kruger National Park rely strongly on herbaceous vegetation in their diet, as was demonstrated using carbon stable isotopes (Codron et al. 2006, Pretorius et al. 2011). Although elephants feed on a great variety of species, they exhibit selectivity in regards to plant parts and nutrient content. Therefore, while we show elephants prefer grass-dominated landscapes in Etosha, they might be selecting small woody plants within these patches (Goheen and Palmer 2010, Pretorius et al. 2011, Biru and Bekele 2012, Shrader et al. 2012).

Diurnal variation in movement patterns and resource preference

Observed long-term patterns of resource selection arise from individuals' repeated step selection behavior while feeding within and moving between foraging patches (Owen-Smith et al. 2010, Avgar et al. 2013). By combining high temporal resolution movement patterns with landscape information, we gained insights into the behavioral patterns (e.g., drinking, foraging, resting) that might underlie resource preference (Polansky et al. 2013, Gurarie et al. 2016).

Our data reveal a relationship between the diurnal variation in movement speed and diurnal variation in resource preference (Figs. 2A, B, and 4). For example, elephants walked faster in early morning and in the afternoon; times that correspond to the times before and after peak preference for water sources. This may indicate directional travel with increased speed toward or away from water (Chamaille-Jammes et al. 2013).

Wittemyer et al. (2008) demonstrated strong diurnal cycles in the movement step lengths of elephants, with one or more cycles per day. Similar to our results, they showed longest step length in early morning and in the afternoon, times with cool temperatures while still during day light. Additional factors that can affect movement speed, that were not considered here, include thermal regulation, weather conditions, seasonal changes in rainfall, and avoidance of human disturbance or predators (Kinahan et al. 2007*b*, Graham et al. 2009, Garstang et al. 2014).

Diurnal variation in resource selection alluded to the behavioral patterns that lead to these preferences. For example, our observed highest preference for water in evening and night times (Fig. 4C) corresponds to previous field observations that those are indeed the hours elephants drink in Etosha (Du Preez 1977). Elephants walked close to roads around the times they selected water (Fig. 4D); this further indicates that roads are used as low resistance paths between water sources. Peaks in preference for grass biomass in early morning and late afternoon may indicate elephants forage at these times (Fig. 4B). Slow walking speed around midday, together with high preference for NDVI and higher tree cover at this time of day (Figs. 2B and 4A, B, respectively) may indicate elephants rest in shaded areas in midday. Similarly, previous research demonstrated that elephants choose cooler and more shaded landscapes during daytime (Kinahan et al. 2007*a*,*b*, Loarie et al. 2009*a*,*b*).

Seasonal variation in elephants' resource preference

Seasonal variation in movement response to landscape variables illustrated the relative ecological importance of each resource for elephants across seasons (Fig. 5, Table 1). Our findings emphasize the informative ecological insights that can be gained by examining changes in resource selection across time.

Forage availability in Etosha, as measured by MODIS-based NDVI or FPAR, fluctuated in a unimodal annual pattern with one peak around mid-March (Fig. 6). Elephants responded to this fluctuation by increasing preference for *declining* resources: preference for NDVI was most prominent in the dry season (July to August), just before NDVI approached its minimum values in September. Importantly, while elephants track increasing vegetation productivity during migration (Bohrer et al. 2014), we show here that relative preference for a resource does not follow higher availability of the resource, but rather selection of a crucial resource becomes stronger as that resource becomes scarcer. Similarly, preference for permanent water sources increases as rainfall declines and the dry season progresses (Fig. 5G). As rainfall diminishes and seasonal surface water dries up, elephants become increasingly dependent on anthropogenic water sources (van Aarde et al. 2006). Our results suggest that preference is driven by changing seasonal needs for the resource: ecological requirement for a resource rises when the resource availability declines (Forester et al. 2009). Resource selection models that incorporate functional responses to habitat availability would be an additional, rigorous way to test species' response to changing habitat availability (Matthiopoulos et al. 2011).

Elephants prefer high NDVI variance in the wet season, but low NDVI variance in the dry months, a pattern that is inversely correlated to monthly preference for NDVI mean (Fig. 5A). This response to temporal variability of vegetation productivity suggests that when forage is abundant animals explore variable conditions in order to maximize chances to discover greener patches and to locate higher quality forage (Loarie et al. 2009*a*, *b*, Young et al. 2009). In the dry season, however, when food becomes scarcer and less nutritious the goal becomes reducing risk of starvation (Turner et al. 2013). Moreover, the quantity of primary production is often inversely related to its digestible quality and nitrogen content (Codron et al. 2006, Hopcraft et al. 2010). Therefore, areas with high variability and low productivity may have the highest nutrient concentration following the onset of rainfall in the wet season (Hopcraft et al. 2010).

FPAR is also preferred strongly in the hot-dry season (Fig. 5B). FPAR is a proxy for residual photosynthetic activity in herbaceous vegetation that might not be captured by NDVI (Tsalyuk et al. 2017). Toward the end of the dry season, moisture and digestible protein in vegetation are especially valuable.

Our results demonstrate that individuals switch seasonally their preference for landscapes dominated by high biomass of grass, shrubs, or trees (Fig. 5C–E). Elephants have prominent impact on vegetation cover and on woody vegetation (de Beer et al. 2006, Chamaille-Jammes et al. 2007, de Beer and van Aarde 2008). Seasonal fluctuations in resource preference, as demonstrated here, might promote vegetation regeneration and prevent resource overutilization (Wittemyer et al. 2009).

Seasonal shifts in preference of biomass of different vegetation types can reflect seasonal changes in the elephants' diet. Elephants feed extensively on green grasses in the wet season and switch to woody browse in the dry season (Cerling et al. 2006, Wittemyer et al. 2009, Pretorius et al. 2011). Conversely, here we observed a stronger preference for high grass biomass in the dry months. High preference of FPAR in the dry season, a strong predictor of grass biomass, further strengthens this observation. As discussed above, possible explanation for this discrepancy is that in drier habitats preference of herbaceous vegetation is maintained throughout the year (Codron et al. 2006).

There is temporal correspondence between average seasonal movement speed and seasonal variation in resource preference (Figs. 2C, D, and 5). Highest movement speed was observed in November and April, which correspond to the beginning and the end of rainy season, respectively. Garstang et al. (2014) similarly showed changes in elephants' movement speed at the onset and following the transition between dry and wet season. Elephants move slower and have smaller home ranges in the dry season since they are restricted to stay closer to water sources (Loarie et al. 2009*a*,*b*). In the wet season, availability of ephemeral surface water allows exploration of new areas, as indicated by faster movement in this season. Additionally, preference for high variance in vegetation conditions in the wet season suggests elephants explore farther areas, thus move faster on average (Polansky et al. 2013).

Notably, there was seasonal variation in the proximity of elephants to roads, which coincide with the number of tourist vehicles in the reserve (Fig. 5H). Tourism increases in Namibia during the cold-dry season, peaking around August; the tourist season coincides with better conditions of otherwise muddy dirt roads, which also eases movement of elephants. The presence of elephants near roads during the peak of the tourist season may indicate that current density of tourist vehicles in Etosha does not disrupt elephants' behavior. Our method of tracking monthly variation in road preference can be used to gauge future effects of tourism on elephants.

Temporal scale of information integration of resource availability

We detected a distinct response to information of resource availability integrated over different temporal scales in locations familiar to the individual. Elephants moved toward regions where long-term forage availability was favorable; this preference was significantly stronger than response to current conditions (Fig. 7, Table 2).

Most research examines the relationship between wildlife movement and landscape conditions simultaneously, at the time of the animal's passing (Fryxell et al. 2008, Bohrer et al. 2014). However, evolutionary forces, reoccurring behavioral patterns, and spatial memory lead animals to choose movement paths that do not directly correspond to forage conditions at the time of movement (Berger-Tal and Bar-David 2015, Oliveira-Santos et al. 2016). We compared how elephants respond to information on resource availability in each pixel they had previously visited, integrated across three time scales: (1) at the time of the elephant's movement, (2) over one year prior to the movement, and (3) over multitemporal average of resource availability (10 yr). Contrary to our expectation, we found that long-term conditions in an area are more influential in determining movement than current forage conditions. Partially, this might reflect that multitemporal remote sensing vegetation data capture additional information about current vegetation state (Tsalyuk et al. 2017). Overall, these findings imply that elephants select consistent locations that are guided by information about forage availability integrated over long-term temporal scale, rather than respond to immediate forage conditions. For each individual elephant, only information from the exact locations that individual had previously visited was used; this further supports the assumption that the elephants had prior knowledge about the sites.

Elephants have high cognitive abilities and excellent spatial memory (Hart et al. 2008, Polansky et al. 2015). Elephants' habitat selection depends on the spatial scale concerned, indicating the use of spatial memory and informed decisions, which spans large spatial scales (de Knegt et al. 2011). Our results demonstrate elephants' ability to integrate spatial information over long temporal scales to improve their access to stable forage sources. Previous research has demonstrated that older matriarchs have greater ecological knowledge that enables the group to better utilize resources in time of drought and to better respond to predation risk (Foley et al. 2008, McComb et al. 2011). Our results further indicate that memory of forage conditions of previously visited locations may optimize resource utilization in elephants.

Our finding that long-term NDVI information has stronger influence on movement than short-term conditions may explain why patterns of resource selection do not always precisely follow resource availability, as would be expected from optimal foraging theory (Wittemyer et al. 2008, Merkle et al. 2016, Aikens et al. 2017) While information on current availability of resources across space is limited to recently visited locations, reliance on past knowledge about feeding patches with high long-term productivity can increase the probability of finding available forage.

Reliance on long-term information about resource availability is specifically important when quantity and quality of vegetation are low. We demonstrate that the temporal scale on which elephants rely to make movement decisions depends on season. In the dry season, as forage availability declines, long-term NDVI and FPAR are more prominent in determining site selection than recent NDVI/FPAR, while in the wet season the differences among scales are not significant.

CONCLUSIONS

We used high temporal resolution movement data and high temporal and thematic resolution satellite imagery to understand how space and time interact to produce an observed movement path. Our results highlight the importance of temporal variation in determining the relationship between animal movement and underlying environmental variables and emphasize the importance of considering temporal variation and temporal scale in analyzing movement data. Including temporal variation in movement analyses provided valuable insights into the behavioral patterns that lead to resource selection, as well as the ecological role of these resources to the animal in each season, insights that would have been missed if we had not examined patterns at different scales. These insights required the use of long-term information about resource availability changes, continuous over space and time; these data that are most comprehensively obtained from satellite imagery. Therefore, our research emphasizes the importance of long-term high temporal resolution satellite imagery for understanding the temporal variability of wildlife resource selection and movement patterns. Importantly, we show that elephants integrate spatial information, in locations they have previously visited, about resource availability over different temporal scales. Long-term information on forage conditions was more prominent in dictating movement decisions than current conditions, particularly in the dry season. These results highlight the importance of considering long-term memory, and, specifically, spatial cognition, together with information on past landscape conditions to understand wildlife movement.

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LITERATURE CITED

Abrahms, B., et al. 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. Movement Ecology 5:12.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Ares, J. O., and M. Bertiller. 2010. Modeling high-frequency position data of large herbivores with a phase-state model. Ecological Modelling 221:2323–2329.

Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. Journal of Animal Ecology 82:96–106.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Baxter, P. W. J., and W. M. Getz. 2005. A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. Ecological Applications 15:1331–1341.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Berger-Tal, O., and S. Bar-David. 2015. Recursive movement patterns: review and synthesis across species. Ecosphere 6:1–12.

Biru, Y., and A. Bekele. 2012. Food habits of African elephant (*Loxodonta africana*) in Babile Elephant Sanctuary, Ethiopia. Tropical Ecology 53:43–52.

Boettiger, A. N., G. Wittemyer, R. Starfield, F. Volrath, I. Douglas-Hamilton, and W. M. Getz. 2011. Inferring ecological and behavioral drivers of African elephant movement using a linear filtering approach. Ecology 92:1648–1657.

Bohrer, G., P. S. Beck, S. M. Ngene, A. K. Skidmore, and I. Douglas-Hamilton. 2014. Elephant movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape. Movement Ecology 2:2.

Boone, R. B., S. J. Thirgood, and J. G. C. Hopcraft. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87:1987–1994.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bracis, C., and T. Mueller. 2017. Memory, not just perception, plays an important role in terrestrial mammalian migration. Proceedings of the Royal Society B 284:20170449.

Butterfield, H. S., and C. M. Malmstrom. 2009. The effects of phenology on indirect measures of aboveground biomass in annual grasses. International Journal of Remote Sensing 30:3133–3146.

Byrne, M. E., J. Clint McCoy, J. W. Hinton, M. J. Chamberlain, and B. A. Collier. 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. Journal of Animal Ecology 83:1234–1243.

Cerling, T. E., G. Wittemyer, H. B. Rasmussen, F. Vollrath, C. E. Cerling, T. J. Robinson, and I. Douglas-Hamilton. 2006. Stable isotopes in elephant hair document migration patterns and diet changes. Proceedings of the National Academy of Sciences USA 103:371–373.

Chamaille-Jammes, S., M. Valeix, and H. Fritz. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. Journal of Applied Ecology 44:625–633.

Chamaille-Jammes, S., G. Mtare, E. Makuwe, and H. Fritz. 2013. African elephants adjust speed in response to surface-water constraint on foraging during the dry-season. PLoS ONE 8:1–6.

Codling, E., and N. Hill. 2005. Sampling rate effects on measurements of correlated and biased random walks. Journal of Theoretical Biology 233:573–588.

Codron, J., J. A. Lee-Thorp, M. Sponheimer, D. Codron, R. C. Grant, and D. J. de Ruiter. 2006. Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. Journal of Mammalogy 87:27–34.

Codron, J., D. Codron, M. Sponheimer, K. Kirkman, K. J. Duffy, E. J. Raubenheimer, J. Melice, R. Grant, M. Clauss, and J. A. Lee-Thorp. 2012. Stable isotope series from elephant ivory reveal lifetime histories of a true dietary generalist. Proceedings of the Royal Society B 279:2433–2441.

Coverdale, T. C., T. R. Kartzinel, K. L. Grabowski, R. K. Shriver, A. A. Hassan, J. R. Goheen, T. M. Palmer, and R. M. Pringle. 2016. Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. Ecology 97:3219–3230.

Darvishzadeh, R., A. Skidmore, M. Schlerf, C. Atzberger, F. Corsi, and M. Cho. 2008. LAI and chlorophyll estimation for a heterogeneous grassland using hyperspectral measurements. ISPRS Journal of Photogrammetry and Remote Sensing 63:409–426.

de Beer, Y., and R. J. van Aarde. 2008. Do landscape heterogeneity and water distribution explain aspects of elephant home range in Southern Africa's and savannas? Journal of Arid Environments 72:2017–2025.

de Beer, Y., W. Kilian, W. Versfeld, and R. J. van Aarde. 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. Journal of Arid Environments 64:412–421.

de Knegt, H. J., et al. 2011. The spatial scaling of habitat selection by African elephants. Journal of Animal Ecology 80:270–281.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, and P. J. Leitão. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027–046.

Douglas-Hamilton, I., T. Krink, and F. Vollrath. 2005. Movements and corridors of African elephants in relation to protected areas. Naturwissenschaften 92:158–163.

Du Plessis, W. P. 1999. Linear regression relationships between NDVI, vegetation and rainfall in Etosha National Park, Namibia. Journal of Arid Environments 42:235–260.

Du Preez, I. 1977. Drinking times and behaviour at waterholes of some game species in the Etosha National Park. Madoqua 10:61–69.

Duffy, K. J. 2011. Simulations to investigate animal movement effects on population dynamics. Natural Resource Modeling 24:48–60.

ESRI. 2011. ArcGIS desktop. Release 10.2. Environmental Systems Research Institute, Redlands, California, USA.

Fagan, W. F., et al. 2013. Spatial memory and animal movement. Ecology Letters 16:1316–1329.

Fishlock, V., C. Caldwell, and P. C. Lee. 2016. Elephant resource-use traditions. Animal Cognition 19:429–433.

Fleming, C. H., J. M. Calabrese, T. Mueller, K. A. Olson, P. Leimgruber, and W. F. Fagan. 2014. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. American Naturalist 183:E154–E167.

Foley, C., N. Pettorelli, and L. Foley. 2008. Severe drought and calf survival in elephants. Biology Letters 4:541–544.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State–space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fortin, D., J. A. Merkle, M. Sigaud, S. G. Cherry, S. Plante, A. Drolet, and M. Labrecque. 2015. Temporal dynamics in the foraging decisions of large herbivores. Animal Production Science 55:376–383.

Franz, M., S. Kramer-Schadt, W. Kilian, C. Wissel, and J. Groeneveld. 2010. Understanding the effects of rainfall on elephant-vegetation interactions around waterholes. Ecological Modelling 221:2909–2917.

Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. Ecology 85:2429–2435.

Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters 8:328–335.

Fryxell, J. M., M. Hazell, L. Borger, B. D. Dalziel, D. T. Haydon, J. M. Morales, T. McIntosh, and R. C. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences USA 105:19114–19119.

Garstang, M., R. E. Davis, K. Leggett, O. W. Frauenfeld, S. Greco, E. Zipser, and M. Peterson. 2014. Response of African elephants (*Loxodonta africana*) to seasonal changes in rainfall. PLoS ONE 9:e108736.

Gautestad, A. O. 2011. Memory matters: Influence from a cognitive map on animal space use. Journal of Theoretical Biology 287:26–36.

Gautestad, A. O., and I. Mysterud. 2010*a*. The home range fractal: From random walk to memory-dependent space use. Ecological Complexity 7:458–470.

Gautestad, A. O., and I. Mysterud. 2010*b*. Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. Ecological Modelling 221:2741–2750.

Getz, W. M., and D. Saltz. 2008. A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences USA 105:19066–19071.

Getz, W. M., R. Salter, A. J. Lyons, and N. Sippl-Swezey. 2015. Panmictic and clonal evolution on a single patchy resource produces polymorphic foraging guilds. PLoS ONE 10: e0133732.

Getz, W. M., R. Salter, D. P. Seidel, and P. van Hooft. 2016. Sympatric speciation in structureless environments. BMC Evolutionary Biology 16:50.

Getz, W. M., W. Kilian, R. Zidon, and M. Tsalyuk. 2018. Data from: Temporal variation in resource selection of African elephants follows long term variability in resource availability. Movebank Data Repository. https://doi.org/10.5441/001/1.3nj3qj45

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710.

Goheen, J. R., and T. M. Palmer. 2010. Defensive plant-ants stabilize megaherbivore-driven landscape change in an African savanna. Current Biology 20:1768–1772.

Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology 79:372–382.

Graham, M. D., I. Douglas-Hamilton, W. M. Adams, and P. C. Lee. 2009. The movement of African elephants in a human-dominated land-use mosaic. Animal Conservation 12:445–455.

Gurarie, E., R. D. Andrews, and K. L. Laidre. 2009. A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:395–408.

Gurarie, E., C. Bracis, M. Delgado, T. D. Meckley, I. Kojola, and C. M. Wagner. 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements. Journal of Animal Ecology 85:69–84.

Hart, B. L., L. A. Hart, and N. Pinter-Wollman. 2008. Large brains and cognition: where do elephants fit in? Neuroscience and Biobehavioral Reviews 32:86–98.

Hijmans, R. J. 2017. raster: Geographic Data Analysis and Modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster

Hooten, M., E. Hanks, D. Johnson, and M. Alldredge. 2014. Temporal variation and scale in movement-based resource selection functions. Statistical Methodology 17:82–98.

Hopcraft, J. G. C., H. Olff, and A. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25:119–128.

Hurley, M. A., M. Hebblewhite, J. M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society B 369:20130196.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C. J., K. Parker, D. Heard, and M. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

Kinahan, A., S. L. Pimm, and R. J. Van Aarde. 2007*a*. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. Journal of Thermal Biology 32:47–58.

Kinahan, A., R. Inge-Moller, P. W. Bateman, A. Kotze, and M. Scantlebury. 2007*b*. Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). Physiology & Behavior 92:560–565.

Knyazikhin, Y., J. Glassy, J. L. Privette, Y. Tian, A. Lotsch, Y. Zhang, Y. Wang, J. T. Morisette, P. Votava, and R. B. Myneni. 1999. MODIS leaf area index (LAI) and fraction of photosynthetically active radiation absorbed by vegetation (FPAR) product (MOD15) algorithm theoretical basis document. http://eospso.gsfc.nasa.gov/atbd/modistables.html

Le Roux, C. J. G., J. O. Grunow, J. W. Morris, G. J. Bredenkamp, and J. C. Scheepers. 1988. A classification of the vegetation of the Etosha National Park South-West Africa. South African Journal of Botany 54:1–10.

Leblond, M., C. Dussault, and J. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. Ecography 33:1102–1112.

Loarie, S. R., R. J. van Aarde, and S. L. Pimm. 2009*a*. Elephant seasonal vegetation preferences across dry and wet savannas. Biological Conservation 142:3099–3107.

Loarie, S. R., R. J. Van Aarde, and S. L. Pimm. 2009*b*. Fences and artificial water affect African savannah elephant movement patterns. Biological Conservation 142:3086–3098.

LP DAAC. 2000–2014. MOD13Q1, MOD15A2 Version006. NASA Land Processes Distributed Active Archive Center, Sioux Falls, South Dakota, USA.

Machwitz, M., U. Gessner, C. Conrad, U. Falk, J. Richters, and S. Dech. 2015. Modelling the gross primary productivity of West Africa with the regional biomass model RBM, using optimized 250 m MODIS FPAR and fractional vegetation cover information. International Journal of Applied Earth Observation and Geoinformation 43:177–194.

Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalized functional responses for species distributions. Ecology 92:583–589.

McComb, K., C. Moss, S. M. Durant, L. Baker, and S. Sayialel. 2001. Matriarchs as repositories of social knowledge in African elephants. Science 292:491–494.

McComb, K., G. Shannon, S. M. Durant, K. Sayialel, R. Slotow, J. Poole, and C. Moss. 2011. Leadership in elephants: the adaptive value of age. Proceedings of the Royal Society B 278:3270–3276.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B 283:20160456.

Mevik, B. H., and H. R. Cederkvist. 2004. Mean squared error of prediction (MSEP) estimates for principal component regression (PCR) and partial least squares regression (PLSR). Journal of Chemometrics 18:422–429.

Moleón, M., C. Martínez-Carrasco, O. C. Muellerklein, W. M. Getz, C. Muñoz-Lozano, and J. A. Sánchez-Zapata. 2017. Carnivore carcasses are avoided by carnivores. Journal of Animal Ecology 86:1179–1191.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052–19059.

Nathan, R., O. Spiegel, S. Fortmann-Roe, R. Harel, M. Wikelski, and W. M. Getz. 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. Journal of Experimental Biology 215:986–996.

Oliveira-Santos, L. G. R., J. D. Forester, U. Piovezan, W. M. Tomas, and F. A. Fernandez. 2016. Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology 85:516–524.

Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. South African Journal of Wildlife Research 26:107–112.

Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B 365:2267–2278.

Panzacchi, M., B. Van Moorter, O. Strand, M. Saerens, I. Kivimäki, C. C. St. Clair, I. Herfindal, and L. Boitani. 2016. Predicting the continuum between corridors and barriers to animal movements using step selection functions and randomized shortest paths. Journal of Animal Ecology 85:32–42.

Pettorelli, N. 2013. The normalized difference vegetation index. Oxford University Press, Oxford, UK.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Plank, M. J., and E. A. Codling. 2009. Sampling rate and misidentification of Lévy and non-Lévy movement paths. Ecology 90:3546–3553.

Plank, M. J., and E. Codling. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: reply. Ecology 92:1701–1702.

Polansky, L., G. Wittemyer, P. C. Cross, C. J. Tambling, and W. M. Getz. 2010. From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. Ecology 91:1506–1518.

Polansky, L., I. Douglas-Hamilton, and G. Wittemyer. 2013. Using diel movement behavior to infer foraging strategies related to ecological and social factors in elephants. Movement Ecology 1:13.

Polansky, L., W. Kilian, and G. Wittemyer. 2015. Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. Proceedings of the Royal Society B 282:20143042.

Pretorius, Y., et al. 2011. Soil nutrient status determines how elephant utilize trees and shape environments. Journal of Animal Ecology 80:875–883.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

R Core Team. 2018. R: a language and environment for statistical computing version 3.3. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Redfern, J. V., R. Grant, H. Biggs, and W. M. Getz. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology 84:2092–2107.

Riginos, C., and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. Ecology 89:2228–2238.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338–1350.

Shrader, A. M., C. Bell, L. Bertolli, and D. Ward. 2012. Forest or the trees: At what scale do elephants make foraging decisions? Acta Oecologica 42:3–10.

Soberon, J., and M. Nakamura. 2009. Niches and distributional areas: Concepts, methods, and assumptions. Proceedings of the National Academy of Sciences USA 106:19644–19650.

Sukumar, R. 2003. The living elephants: evolutionary ecology, behavior, and conservation. Oxford University Press, New York, New York, USA.

Therneau, T. 2015. A package for survival analysis in S. version 2.38. https://CRAN.R-project.org/package=survival

Thouless, C. R., H. T. Dublin, J. J. Blanc, D. P. Skinner, T. E. Daniel, R. D. Taylor, F. Maisels, H. L. Frederick, and P. Bouche. 2016. African elephant status report 2016: an update from the African elephant database. Report No. 60 IUCN/SSC. African Elephant Specialist Group. IUCN, Gland, Switzerland.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

Tsalyuk, M., M. Kelly, K. Koy, W. M. Getz, and H. S. Butterfield. 2015. Monitoring the impact of grazing on rangeland conservation easements using MODIS vegetation indices. Rangeland Ecology & Management 68:173–185.

Tsalyuk, M., M. Kelly, and M. W. Getz. 2017. Improving the prediction of African savanna vegetation variables using time series of MODIS products. ISPRS Journal of Photogrammetry and Remote Sensing 131:77–91.

Turner, W. C., P. Imologhome, Z. Havarua, G. P. Kaaya, J. K. E. Mfune, I. D. T. Mpofu, and W. M. Getz. 2013. Soil ingestion, nutrition and the seasonality of anthrax in herbivores of Etosha National Park. Ecosphere 4:art13.

Turner, W. C., and W. M. Getz. 2010. Seasonal and demographic factors influencing gastrointestinal parasitism in ungulates of Etosha National Park. Journal of Wildlife Diseases 46:1108–1119.

van Aarde, R. J., T. P. Jackson, and S. M. Ferreira. 2006. Conservation science and elephant management in southern Africa. South African Journal of Science 102:385–388.

van Beest, F. M., E. V. Wal, A. V. Stronen, P. C. Paquet, and R. K. Brook. 2013. Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. Oecologia 173:409–420.

Van Moorter, B., C. M. Rolandsen, M. Basille, and J. Gaillard. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21–31.

Vanak, A. T., M. Thaker, and R. Slotow. 2010. Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? Biological Conservation 143:2631–2637.

Wittemyer, G., L. Polansky, I. Douglas-Hamilton, and W. M. Getz. 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. Proceedings of the National Academy of Sciences USA 105:19108–19113.

Wittemyer, G., T. E. Cerling, and I. Douglas-Hamilton. 2009. Establishing chronologies from isotopic profiles in serially collected animal tissues: An example using tail hairs from African elephants. Chemical Geology 267:3–11.

Wolf, A., C. E. Doughty, and Y. Malhi. 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. PLoS ONE 8:e71352.

Young, K. D., S. M. Ferreira, and R. J. van Aarde. 2009. Elephant spatial use in wet and dry savannas of southern Africa. Journal of Zoology 278:189–205.

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1348/full

DATA AVAILABILITY

Location data are available from Movebank: https://doi.org/10.5441/001/1.3nj3qj45. MODIS data version V006 available for years 2000–2014 from the online Data Pool, courtesy of the NASA Land Processes Distributed Active Archive Center (LP DAAC 2000–2014). All data can be downloaded for free from Earthdata tool: https://search.earthdata.nasa.gov/search/. Normalized Difference Vegetation Index (NDVI) MOD13Q1 data product is part of MODIS/Terra Vegetation Indices 16-Day L3 Global 250 m SIN Grid V006. Fraction of Photosynthetically Active Radiation (FPAR) MOD15A2H data product is part of MODIS/Terra Leaf Area Index/FPAR 8-Day L4 Global 500 m SIN Grid V006.