In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration

Hattie L. A. Bartlam-Brooks,[1,2] Pieter S. A. Beck,[2,3] Gil Bohrer,[4] and Stephen Harris[1]

[1] Historically, ungulate migrations occurred in most grassland and boreal woodland ecosystems, but many have been lost due to increasing habitat loss and fragmentation. With the rate of environmental change increasing, identifying and prioritizing migration routes for conservation has taken on a new urgency. Understanding the cues that drive long-distance animal movements is critical to predicting the fate of migrations under different environmental change scenarios and how large migratory herbivores will respond to increasing resource heterogeneity and anthropogenic influences. We used an individual-based modeling approach to investigate the influence of environmental conditions, monitored using satellite data, on departure date and movement speed of migrating zebras in Botswana. Daily zebra movements between dry and rainy season ranges were annotated with coincident observations of precipitation from the Tropical Rainfall Measuring Mission data set and Moderate Resolution Imaging Spectroradiometer-derived normalized difference vegetation index (NDVI). An array of increasingly complex movement models representing alternative hypotheses regarding the environmental cues and controls for movement was parameterized and tested. The best and most justified model predicted daily zebra movement as two linear functions of precipitation rate and NDVI and included a modeled departure date as a function of cumulative precipitation. The model was highly successful at replicating both the timing and pace of seven actual migrations observed using GPS telemetry ($R^2 = 0.914$). It shows how zebras rapidly adjust their movement to changing environmental conditions during migration and are able to reverse migration to avoid adverse conditions or exploit renewed resource availability, a nomadic behavior which should lend them a degree of resilience to climate and environmental change. Our results demonstrate how competing individual-based migration models, informed by freely available satellite data, can be used to evaluate the weight of evidence for multiple hypotheses regarding the use of environmental cues in animal movement. This modeling framework can be applied to quantify how animals adapt the timing and pace of their movements to prevailing environmental conditions and to forecast migrations in near real time or under alternative environmental scenarios.

1. Introduction

[2] Ungulate migrations are iconic wildlife events that historically occurred globally in the majority of grassland and boreal woodland ecosystems [*Dingle*, 1996]. Ultimate benefits for migratory ungulates include exploiting seasonal changes in forage abundance or quality [*Boone et al.*, 2006], accessing spatially and/or temporally variable limiting resources [*McNaughton*, 1990], and escaping higher predation or parasite pressure [*Folstad et al.*, 1991; *Heard et al.*, 1996]. However, both the proximate reasons for migration and the fitness consequences are poorly understood [*Holdo et al.*, 2009; *Milner-Gulland et al.*, 2011].

[3] Migratory behavior increases extinction risk [*McKinney*, 1997] because large ungulates exploit multiple seasonal habitats, and so they are particularly susceptible to habitat loss and fragmentation [*Harris et al.*, 2009]. Blocking a migratory route or loss of preferred seasonal range is often followed by a catastrophic population decline or the loss of that population [*Bolger et al.*, 2008]. As rates of habitat loss and fragmentation increase across ungulate ranges, identifying and prioritizing migration routes for conservation has taken on a new urgency

[1]School of Biological Sciences, University of Bristol, Bristol, UK.
[2]These authors contributed equally to this work.
[3]Woods Hole Research Center, Falmouth, Massachusetts, USA.
[4]Department of Civil, Environmental and Geodetic Engineering, Ohio State University, Columbus, Ohio, USA.

Corresponding author: H. L. A. Bartlam-Brooks, School of Biological Sciences, University of Bristol, Woodland Rd., Bristol BS8 1UG, UK. (hattie.bartlam@bristol.ac.uk)

[*Sawyer et al.*, 2009]. Developing models that predict migratory movements and forecast animals' whereabouts are key conservation tools for designing optimal corridors and refuges along migration routes and helping evaluate the vulnerability of migrations to population or environmental change [*Berger et al.*, 2008; *Holdo et al.*, 2009].

[4] Anecdotal evidence from before the 1970s describes an annual ~250 km zebra (*Equus burchelli antiquorum*) migration from the southeastern Okavango Delta in Botswana to the Makgadikgadi grasslands at the start of the rainy season (November to April). However, from 1968 to 2004, this migration was blocked by a fence erected to separate wildlife from domestic livestock. Life expectancy of zebras in the wild is about 12 years [*Estes*, 1966], so the 36 year period during which migration was prevented makes it highly improbable that any of the zebras that made the migration historically were still alive in 2004. Nonetheless, within 3 years of the fence being removed, zebras were undertaking highly directed migratory movements from the Okavango Delta to the Makgadikgadi at the start of the rainy season, returning at the end of the rains [*Bartlam-Brooks et al.*, 2011].

[5] The Okavango-Makgadikgadi migratory zebras provide an exceptional opportunity to compare the influence of external, i.e., environmental, versus internal, i.e., physiological, cues in the timing and pace of migration and to use this information to understand the impacts of environmental change on the migration. Uniquely, since these zebras could not have learnt the migratory route or the benefits of a migratory strategy as juveniles, the migration was not a cultural legacy but the rediscovery of a highly directed migratory route and its life history benefits through other means [*Fagan et al.*, 2012].

[6] Timing is critical because the Makgadikgadi grasslands are inhospitable to ungulates before the annual rains have filled the water holes. Were the conditions at the destination to vary periodically, the animals would be expected to rely on an "internal clock" to initiate and pace migratory movement. If they do not, animals might respond to environmental cues to regulate migration provided these are proxies for future conditions at the destination. However, in many ecosystems, including savannahs, spatial coherency among weather systems that control primary productivity varies between years, potentially rendering environmental conditions unreliable proxies for remote habitats. Migration strategies thus need to be adaptable enough to cope with this stochasticity. The so-called "nomadic" animals epitomize this, displaying no discernible migratory pattern but instead following resources that are distributed unpredictably [*Mueller et al.*, 2011a]. In other words, for zebras to optimize the timing and speed of their migration based on environmental conditions in the Okavango Delta, the latter must be useful predictors of environmental conditions 200 km away in the Makgadikgadi grasslands. Furthermore, in years when this is not the case, their migration strategy must allow the animals, at a minimum, to adapt their movement to avoid starvation and ideally be able to move to alternative habitats.

[7] Investigating these facets of migration ecology is challenging in most systems because of the wide spatial and temporal extent of migrations and the remoteness of migratory environments [*Bowlin et al.*, 2010]. Furthermore, events that trigger migration might be local and of short duration and thus hard to detect or distinguish from covarying putative causal variables [*Bauer et al.*, 2011]. Another challenge

lies in relating specific environmental variables encountered during the migration to the combined effect they have on the movement patterns and resulting location of the animal, and how to determine which of many covarying environmental conditions is most probably responsible for the observed behavior. To investigate the drivers of the Okavango-Makgadikgadi migration, we capitalized on the unique ability of Earth-orbiting satellites to document daily animal movements and map environmental conditions at regular temporal intervals. Time series of satellite images have previously been used to compare migration cycles to landscape-scale spatio-temporal patterns in climate and primary productivity [*Wang et al.*, 2010], and weather variables have been used in empirical models of bird migration [*Bohrer et al.*, 2012; *Mandel et al.*, 2011; *Sapir et al.*, 2011]. While remote sensing data have been used in general mammal movement and distribution models [*Boone et al.*, 2006; *Holdo et al.*, 2009; *Pettorelli et al.*, 2011], hitherto they have not been used to model initiation of migration and speed of travel in terrestrial mammals.

[8] Here we develop a conceptual and mathematical framework to translate hypotheses about environmental influences on migration to models of the locations of migrating animals. We then use these models to test which environmental variables and assumed functional relationships are the drivers of the observed movement. We expand upon the approach of individual-based modeling to discern environmental controls on animal movement [*Bunnefeld et al.*, 2011; *Mueller et al.*, 2011b] and model movement as a minimal series of heuristic decision-making rules: Start migration or not? Move faster or slower? We then generate and compare a set of models that are based on alternative hypotheses of how these decisions depend on environmental conditions encountered en route. Each set of hypotheses translates to a unique model that, when given a starting location and time, is able to generate a trajectory through a landscape as it changes through time. By initiating such models using animals' locations prior to migration and comparing resultant trajectories to actual GPS-tracked migrations, support for the hypotheses underlying different models can be evaluated.

[9] Specifically, we use predictive movement models to investigate the role of environmental cues in the timing and speed of the Okavango-Makgadikgadi zebra migration using a combination of GPS data and satellite-derived gridded time series of vegetation productivity and rainfall. We hypothesized that (i) rainfall patterns at the start of the rainy season in the Okavango Delta hold cues on vegetation productivity in the Makgadikgadi grasslands 200 km away; (ii) environmental cues, such as rainfall and vegetation productivity, provide better predictors of the onset of migration than a fixed calendar date; and (iii) environmental data could predict the zebras' migratory movements at a daily time step.

2. Methods

2.1. Zebra Tracking

[10] Seven adult zebra mares were used in this analysis. Only collaring mares does not introduce sex- or age-specific movement biases because female zebras live and migrate in permanent harems. The mares were darted from a stationary vehicle by an experienced wildlife veterinarian and fitted with Global Positioning System (GPS) collars (Vectronic GPS-Plus 4D and Vectronic GPS-Plus IRIDIUM 4D; Vectronic
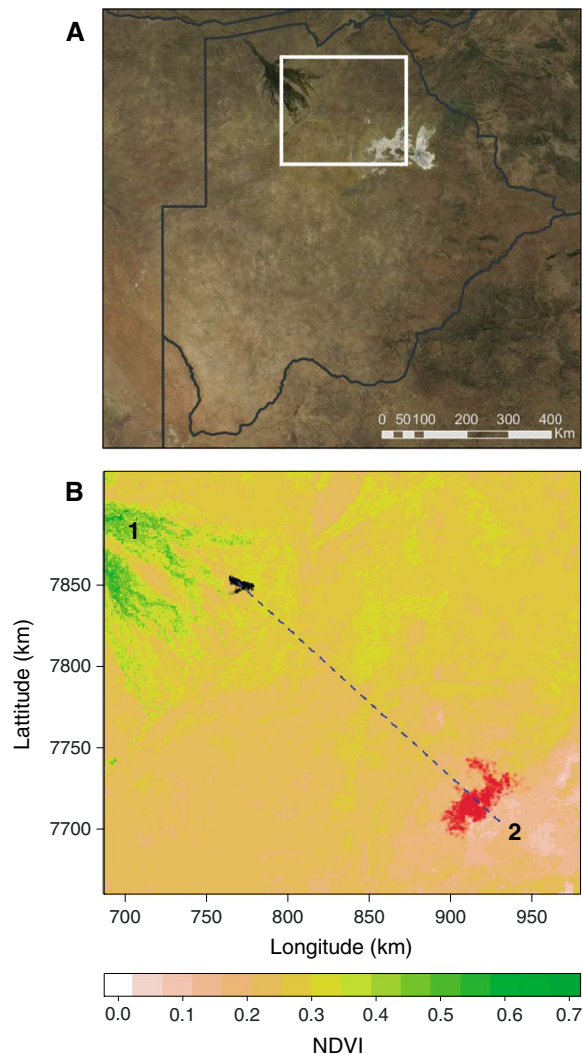
Figure 1. (a) Map and true-color MODIS image of Botswana. The study area between the Okavango Delta in the northwest and the Makgadikgadi in the southeast is highlighted. (b) Mean MODIS NDVI in the study area during the dry August-September periods of 2007 and 2008. The map shows the Universal Transverse Mercator coordinate system (zone 34 south). Dots denote GPS-recorded zebra locations in the dry August-September (black cluster) and the rainy December-January period (red cluster). The blue dashed line indicates the axis along which the zebras migrate from their dry season habitat close to the Okavango Delta (1 on the map) to their rainy season habitat close to the Makgadikgadi (2 on the map).

Aerospace GmbH, Berlin, Germany). The collars weighed 0.95 kg, <0.3% of the total body weight of a southern African zebra mare, and provided hourly geographical fixes. Only 3-D fixes were retained, which accounted for 97% of all fixes, and these were aggregated to a daily resolution [*Bartlam-Brooks et al.*, 2011]. All animal handling procedures were covered by a University of Bristol investigation number (UB/06/012) and by a Botswana research permit (EWT3/3/8XXXIV). The data used in this study are available on Movebank (movebank.org) and are published in the Movebank Data Repository with DOI 10.5441/001/1.f3550b4f.

2.2. Environmental Satellite Data

[11] Normalized difference vegetation index (NDVI) data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) on board NASA's Terra and Aqua satellites (collection 5 of MOD13 and MYD13, respectively [*Huete et al.*, 2002]) were used to describe spatiotemporal variability in vegetation productivity in 2007 and 2008. Productive green vegetation contains pigments that absorb red light but has structural properties that strongly reflect near-infrared light. This unique combination of characteristics means that a simple or normalized ratio of near-infrared and red reflectance can be used to map patterns in gross primary productivity and closely tracks the phenology of leaves [*Pettorelli et al.*, 2005; *Tucker*, 1979].

[12] The MODIS sensor maps red and near-infrared reflectance globally at 232 m spatial resolution and near-daily intervals. Because clouds, aerosols, and variations in Sun-surface-sensor geometry can distort these measurements, daily MODIS NDVI data from each satellite are composited at 16 day intervals. Only the most trusted observation for the 16 days was included for each 232 m grid cell in the MOD13 and MYD13 data available from the Land Processes Distributed Active Archive Center (https://lpdaac.usgs.gov). Data from MOD13 and MYD13 were combined and filtered further using embedded quality flags to retain only observations with the three highest usefulness levels. Since the day with optimal measurement conditions varies, the resulting NDVI time series are temporally irregular because consecutive NDVI observations can be 1 to 30 days apart (15 on average). We used the observation data stored with each NDVI data value to interpolate NDVI time series for each grid cell to daily resolution using univariate Akima interpolation which applies a piecewise function composed of a set of polynomials of third degree or less [*Akima*, 1991]. The interpolation was applied to MODIS time series from 2000 to 2011 to create daily NDVI maps as well as maps of the daily rate of change of NDVI (dNDVI) for the entire study area.

[13] Tropical Rainfall Measuring Mission (TRMM) data from NASA (TRMM-3B42 version 6, http://mirador.gsfc.nasa.gov/) were used to map daily rainfall. The TRMM-3B42 algorithm combines inputs from sensors aboard multiple satellites to generate 3-hourly precipitation (mm/h) at 0.25° (~26 km) spatial resolution [*Huffman et al.*, 2007]. TRMM-3B42 includes passive and active microwave measurements to estimate height and vertical profile of precipitating clouds and infrared radiance measurements to derive top-of-cloud temperatures. The original 3-hourly TRMM rainfall estimates were converted to daily rates and weekly cumulative precipitation. To evaluate the accuracy of TRMM data in our study area, we compared daily rain gauge observations recorded at the border of the Makgadikgadi grasslands (Khumaga Gate, 25.187°E, 20.496°S) with the TRMM values in the coincident grid cell.

[14] We investigated whether rainfall patterns in the zebras' dry season range in the Okavango Delta held reliable cues for vegetation productivity in their rainy season range. In particular, we tested whether cumulative rainfall in the portion of the Okavango Delta used by the zebras in the dry season could predict NDVI patterns in the portion of the Makgadikgadi used by the animals in the rainy season (Figure 1). For this analysis, cumulative rainfall was calculated from 15 September each year, and NDVI values
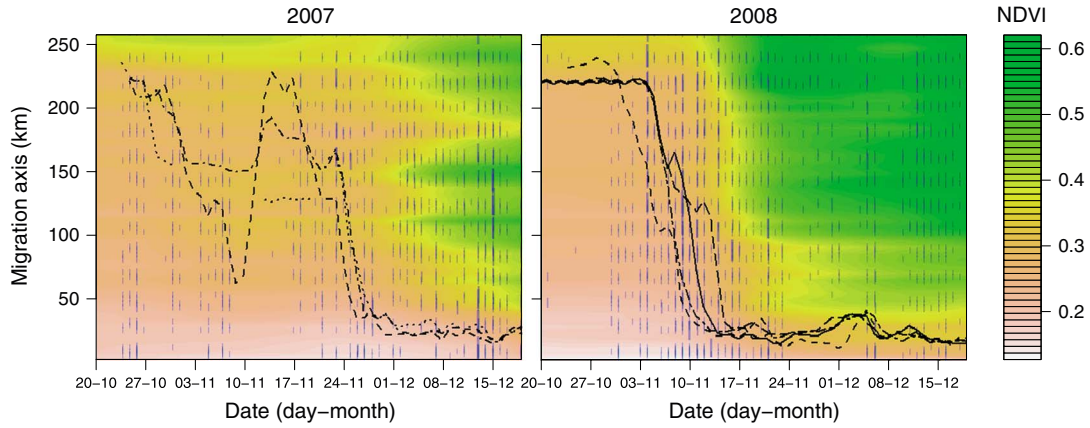
Figure 2. Zebra migrations from the Okavango Delta to the Makgadikgadi at the onset of the rains in 2007 and 2008. The Okavango Delta is at the top of the graphs and the Makgadikgadi is at the bottom. Different black lines indicate the movements of individual collared animals. Blue vertical hashes indicate satellite-observed rainfall in the region during the migration.

prior to the annual NDVI minimum were set to the annual minimum to focus the analysis on the "greening" vegetation likely to be grazed by the animals. A linear regression model was then used to estimate Makgadikgadi NDVI as a function of cumulative rainfall in the Okavango Delta. Model results were compared to a simpler model that estimated square root of NDVI as a linear function of the day of the year in the first part of the rainy season (15 September to 1 February). All means are ±SD.

2.3. Migration Models

[15] We documented three individual migrations in 2007 and four in 2008. The zebra movements were strongly directional, and the area surrounding the migration corridor was dominated by arid scrub of low grazing value. This enabled us to reduce the spatial dimensions of the migration to a single geographical axis and eliminated the need to model the orientation of the migration, as done in more complex movement models [e.g., *Mueller and Fagan*, 2008; *Mueller et al.*, 2011b]. Thus, the zebras' positions were expressed along this "migration axis" (Figure 1b). Its origin was set in the Makgadikgadi and orientation determined by fitting a linear regression model to the latitude and longitude of all zebra positions between October and January. Daily zebra GPS locations were then projected from the two-dimensional geographical space to their position along the one-dimensional migration axis to quantify the daily distance from the rainy season habitat. Spatial patterns in daily rainfall rate, cumulative precipitation, NDVI, and dNDVI were described by calculating their mean values at 5.2 km intervals along the migration axis (Figure 2). Once movements along the migration axis were quantified and annotated with the environmental variables, we tested whether the environmental data could be used to predict the zebras' migratory behavior, particularly the start of migration, the speed, and the direction of movement along the migration axis.

[16] Following the principles of individual-based modeling, we decomposed movement behavior to simple heuristic rules. We then hypothesized how these rules might relate functionally to the environment and translated them to an

array of increasingly complex models that simulate individual animal movements (Table 1). Comparison of the goodness of fit and information criterion of these models was used to determine which hypothesis is the most justified description of the migratory behavior from the Okavango Delta to the Makgadikgadi. The models fitted into three classes:

[17] 1. Internal clock, environmentally invariant models (Table 1, models 1 and 3) which predicted location as a linear or logistic function of the date, with migration starting at a fixed date each year. These models assumed a regular movement pattern and did not include NDVI or rainfall data. Departure date was prescribed as the observed mean (October 30), based on the last time each animal crossed the 210 km mark on the migration axis before November 9. In essence, these models assume that an internal clock caused migration always to start on the same date and can be simply formulated as

$$X = f_i(t - t_{d\_obs}), \tag{1}$$

where X is the location of the animal along the migration axis at time t after the observed mean annual date of the start of migration and t_{d_obs}. $f_i(\_)$ are different hypothetical functional relationships that relate the location to time and can include a linear, quadratic, logarithmic, logistic relationship, etc. (as in *Bunnefeld et al.* [2011]).

[18] 2. Models that predicted the start of migration as a function of environmental variables (models 2 and 4) and continue migration at a fixed rate. These models add an additional set of hypotheses to the previous class of models, namely that the time of departure t_d occurs when a certain environmental condition C_i is met

$$\begin{cases} t_0 = t_d | C_i \\ X = f_i(t - t_0) \end{cases} \tag{2}$$

C_i describes a set of alternative hypotheses that relate the heuristic decision of whether to start migrating now or not to some function of the environment. Using the observed departure dates (as defined above) as reference, we found that

Table 1. Empirical Models Predicting Seasonal Movement From the Okavango Delta Toward the Makgadikgadi Pans[a]

	Model Name	N	Model Equation	R^2	AIC	a_1	a_2	a_3	a_4	a_5
1	Linear	1	$X = X_d + a_2(t - t_{d\_obs})$	0.680	2,525		−9,174.26			
2	Linear + departure	2	$X = X_d + a_2(t - t_{sp})$	0.581	942	251	−9,259.47			
3	Logistic	2	$X = \dfrac{(X_d - X_e)}{(1 + \exp(a_3(a_2 + (t - t_{d\_obs}))))} + X_e$	0.690	897		−19.579	0.183		
4	Logistic + departure	3	$X = \dfrac{(X_d - X_e)}{(1 + \exp(a_3(a_2 + (t - t_{sp}))))} + X_e$	0.590	934	251	−8.864	0.165		
5	Linear dynamic NDVI	3	$\frac{dX}{dt} = a_3 + a_2\mathrm{NDVI} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.903	767	251	43.585	−132,184.99		
6	Linear dynamic dNDVI	3	$\frac{dX}{dt} = a_3 + a_2\frac{d\mathrm{NDVI}}{dt} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.760	874	251	−176.74	−3,771.34		
7	Linear dynamic precip	3	$\frac{dX}{dt} = a_3 + a_2\mathrm{precip} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.861	806	251	−10.407	−2,611.63		
8	Linear dynamic cumulative precip	3	$\frac{dX}{dt} = a_3 + a_2\sum\mathrm{precip} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.882	789	251	−4.235	−335.32		
9	Quadratic dynamic NDVI	4	$\frac{dX}{dt} = a_4 + a_2\mathrm{NDVI}^2 + a_3\mathrm{NDVI} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.907	763	251	0.017	−51.53	−49.39	
10	**Linear dynamic NDVI and precip**	4	$\frac{dX}{dt} = a_4 + a_3\mathrm{precip} + a_2\mathrm{NDVI} \mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.914	752	251	24.954	−4.715	−76,411.6	
11	Linear dynamic NDVI, precip and interaction	5	$\frac{dX}{dt} = a_4 + a_3\mathrm{precip} + a_2\mathrm{NDVI} + a_5\mathrm{precip} \times \mathrm{NDVI}$ $\mid X_0 = X_d; X_{end} = X_e; t_0 = t_{sp}$	0.915	754	251	24.569	−6.813	−75,276.9	0.0007

[a]Where n is the number of parameters, X is the location in meters along an axis from the Makgadikgadi Pans to the Okavango Delta, X_d is the observed mean location of departure (210,000 m), X_e is the mean observed location of the end of the migration (25,000 m), t is time in days, t_{d_obs} is the mean observed day of departure, $t_{sp} = t_d(|\sum\mathrm{precip}_{>a_1}|)$ is the time of departure using a departure date model as a function of 7 day cumulative precipitation $\sum\mathrm{precip}$, precip is the precipitation rate in millimeters scaled by a factor 100, NDVI is the normalized difference vegetation index scaled by a factor 10,000, X_0 and X_{end} are the spatial boundary conditions, t_0 is the start time of the dynamic model, and a_1, a_2, a_3, a_4, and a_5 are the model parameters. All models were significant at $P < 0.0001$. The most justified model is highlighted in bold. The model parameters, statistics of goodness of fit (R^2) between models and observations, and the Akaike information criterion (AIC) of each model are presented. The model ranked best, in terms of highest R^2 and lowest AIC, is highlighted in bold type.
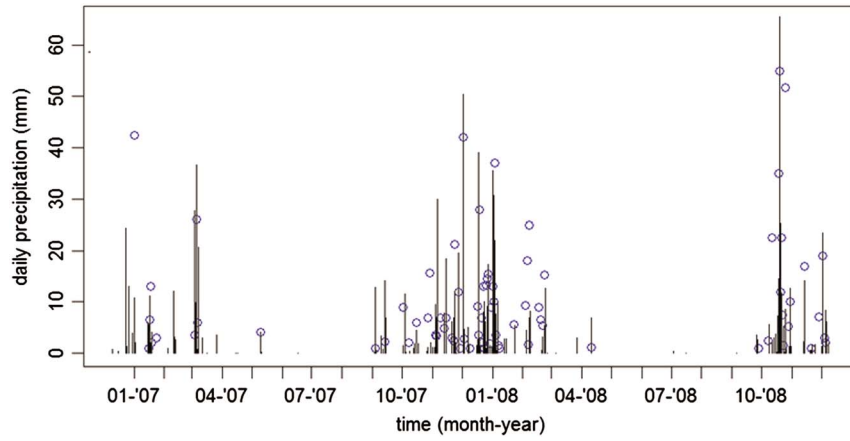
Figure 3. Daily rainfall in the Makgadikgadi in 2007 and 2008 measured by satellite and a rain gauge. Blue circles indicate the rainfall measured at the Khumaga meteorological station and the black lines indicate rainfall measured by the Tropical Rainfall Measuring Mission and Other Satellites Precipitation Product (TRMM-3B42 version 6) in the coincident 650 km^2 grid cell.

only cumulative precipitation was useful in predicting the start of migration and that the other environmental variables (NDVI, dNDVI, and precipitation rate) could not improve the prediction. Consequently, we determined the threshold value of weekly cumulative precipitation that, once exceeded, caused the zebras to start to migrate.

[19] 3. Environmentally dependent movement models (models 5–11). As opposed to models in classes 1 and 2 that hypothesize a functional relationship between environmental conditions and the location of the animal directly, the third class of models is based on the assumption that environmental conditions only affect the components of movement and that a sequence of movement steps then integrates to a time series of locations. In these agent-based models, movement speed was determined daily as a function of the environmental variables. While the parameters of the function f_i relating environmental variables to movement speed were assumed constant, the resulting movement was not at constant speed because environmental variables E_i vary spatiotemporally. These models have the general form

$$\begin{cases} \dfrac{dX}{dt} = f_i(\{E_i\} | (t_0 = t_d | Ci)) \\ X = \displaystyle\int_{X_0 = B_1}^{X_{\text{end}} = B_2} \dfrac{dX}{dt} dt \end{cases}, \quad (3)$$

where movement speed is the rate of change of location dX/dt and mathematically analogous to the first derivative of location. $f_i()$ is a set of hypothetical functional relationships between the speed and a set of environmental conditions, E_i, such as precipitation rate and vegetation productivity. C_i is a set of environmental conditions for the time at which to start the simulation, which was determined to be driven by cumulative precipitation, as in (2). We assumed f_i to be a linear function, and $\{E_i\}$ included NDVI, dNDVI, precipitation rate, and certain quadratic forms and interactions of these variables. B_1 and B_2 are general assumptions regarding the boundary conditions of the integration, i.e., the start and end locations, respectively. All models assumed that each zebra's location before departure was the mean location

recorded for it between October 20 and 25 (X_d), i.e., $X_0 = B_1 = X_d$. We assumed that a migration ended when the zebras' average position in the Makgadikgadi between 25 November and 2 December (X_e) was reached, i.e., km 25 on the migration axis, $X_{\text{end}} = B_2 = X_e$.

[20] In all models, we estimated the parameters using the function *fmincon* for nonlinear constrained optimization in MATLAB version 7.9 [*Han*, 1977]. We used randomly chosen parameter values to initiate the optimization to avoid convergence to local minima. The Akaike information criterion (AIC) with a correction for sample size [*Akaike*, 1974] was used to reconcile a model's goodness of fit (R^2) with its number of parameters and identify the most justified model.

3. Results

3.1. Spatiotemporal Coherency Between Rainfall and Vegetation Productivity

[21] Despite disparate footprints, daily precipitation rates (DPR) in 2007 and 2008 measured by TRMM (650 km^2 grid cells) and the Khumaga rain gauge (0.1 m^2 opening) agreed reasonably well ($R = 0.57$, $P < 0.001$, d.f. $= 129$, Figure 3). Overall, TRMM described more days with low rainfall and fewer days with very high rainfall than recorded at Khumaga ($\text{DPR}_{\text{TRMM}} = 0.56 \pm 0.07 \times \text{DPR}_{\text{gauge}} + 4.47 \pm 0.84$). This was to be expected, given the large area integrated in a TRMM grid cell and the dominance of localized rainfall in semiarid ecosystems. Rainfall rates recorded by TRMM over the Okavango Delta during the rainy season (15 September to 1 February) averaged 4.3 ± 10 mm/d in 2007–2008 and 3.7 ± 8.3 mm/d in 2008–2009. These were the highest rates between 2000 and 2011; the lowest rate was in 2000–2001 (1.2 ± 5.5 mm/d), the only rainy season in which Makgadikgadi rainfall rates (1.5 ± 4.1 mm/d) exceeded those in the Okavango Delta.

[22] The Okavango Delta and Makgadikgadi displayed highly consistent annual precipitation ($R^2 = 0.79$, $N = 11$), but daily rainfall rates were less correlated ($R^2 = 0.47$, $N = 4099$, Figure 4). Nonetheless, precipitation in the Okavango Delta at the start of the rainy season was indicative
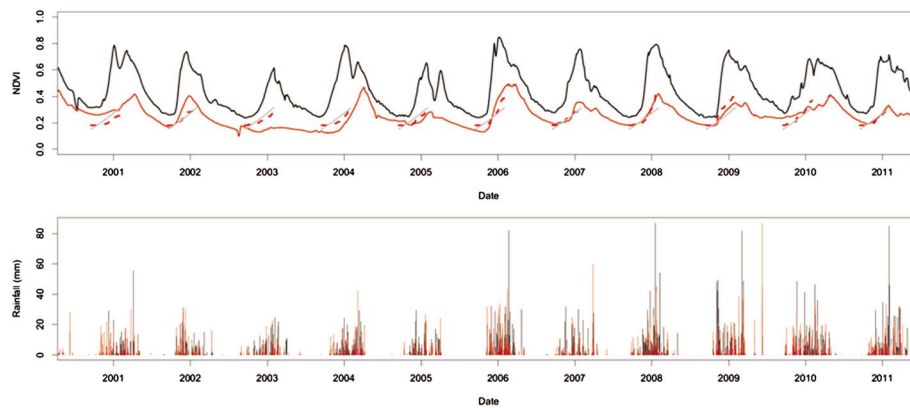
Figure 4. NDVI and rainfall in the Okavango Delta and Makgadikgadi during the dry and rainy seasons, respectively. Data are for the portion of the Okavango Delta used by the migratory zebras in the dry season (black lines here, black dots in Figure 1) and in the section of the Makgadikgadi grasslands used by the zebras in the rainy season (red lines here, red dots in Figure 1). Red dotted lines show NDVI estimates for the Makgadikgadi during the dry season-rainy season transition and generated by a linear regression model with cumulative precipitation in the Okavango Delta as independent variable. Grey lines show similar NDVI estimates but produced using a regression model with the day of the year as independent variable.

of future vegetation productivity in the Makgadikgadi. The regression model that predicted Makgadikgadi NDVI as a function of cumulative precipitation since 15 September explained 57% of the variance, 17% more than the model that relied solely on time of the year (Figure 4). Performance of the model varied between years (as indicated by analysis of variance of annual residuals, $P < 0.001$), depending on the spatiotemporal coherency between weather systems over the dry and wet season habitats. For example, in 2007, initial rainfall in late October and early November was not sustained in mid-November, causing only moderate increases in NDVI, and widespread greening of the landscape was delayed until early December. In response, one collared zebra (M3) returned

approximately 150 km to the Okavango despite being less than 70 km from the Makgadikgadi grasslands (Figure 5). Conversely, when returning to the Okavango Delta in April 2009, M3 retraced its steps ~50 km following unseasonally late rainfall in the Makgadikgadi (Figure 6).

[23] In contrast, heavy rains on 4 November 2008 were sustained for the three subsequent weeks, leading to "green-up" by mid-November. In 2008, the simple rainfall model predicted NDVI values in the Makgadikgadi to increase on average 19 ± 6 days earlier than they did because the area did not receive the large rainfall events that occurred in the Okavango Delta at the start of the 2008–2009 rainy season (Figure 4). Rainfall patterns at the start
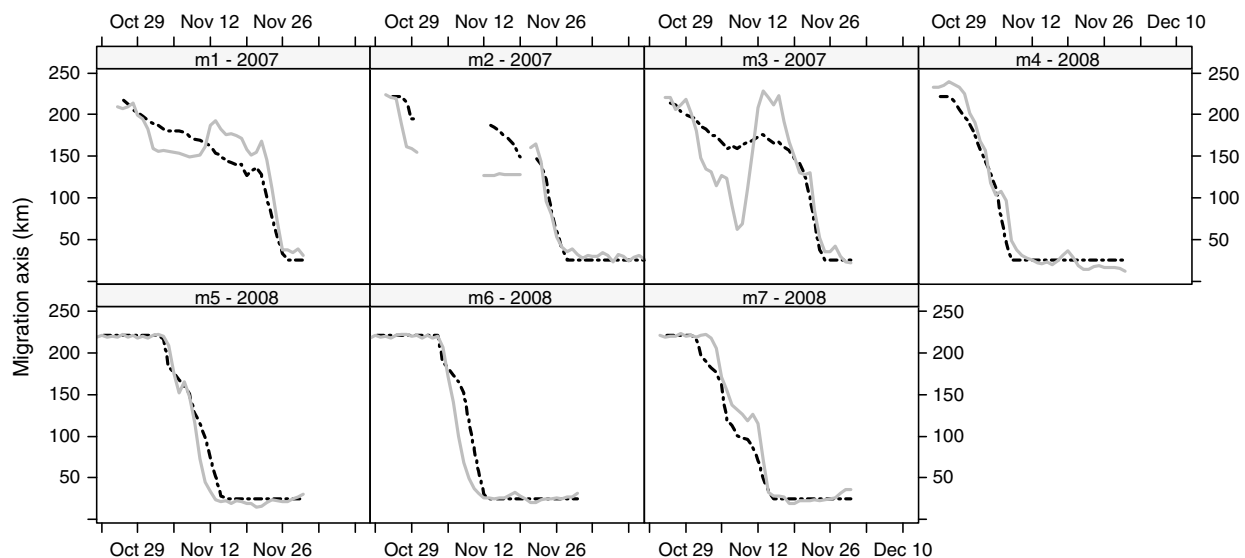

Figure 5. Seven zebra migrations from the Okavango Delta to the Makgadikgadi during 2007 and 2008. Grey solid lines denote movements measured with GPS-equipped collars and black dashed lines denote the movements predicted using a movement model driven by vegetation productivity and rainfall derived from satellite data (Table 1, model 10).
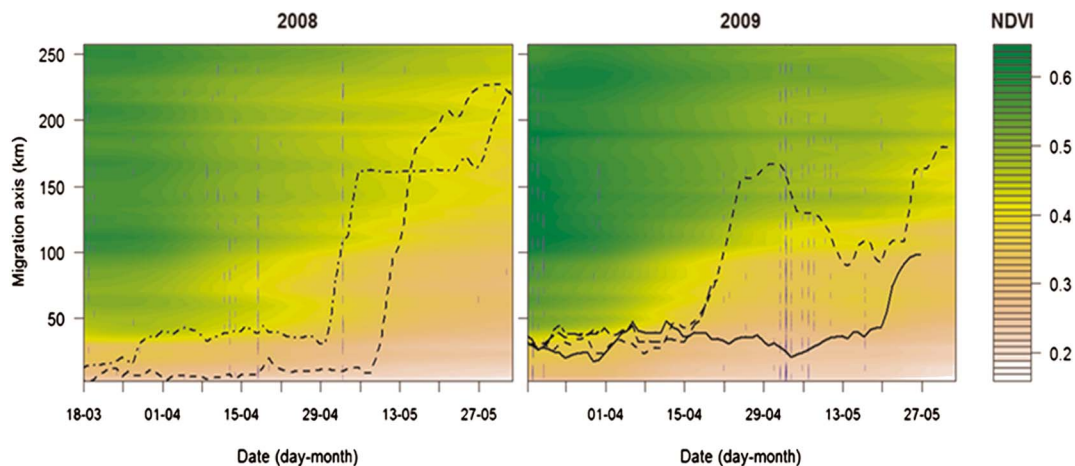
Figure 6. Return zebra migrations from the Makgadikgadi to the Okavango Delta in the dry seasons of 2008 and 2009. The Okavango Delta is at the top of the graphs and the Makgadikgadi is at the bottom. Different black lines indicate the movements of individual collared animals. Blue vertical dashes represent satellite-observed rainfall in the region during the migration. Movement models were not developed for this leg of the migration due to the low sample size.

of the 2007–2008 rainy season were more coherent between the two areas, causing the model to perform better (NDVI values were observed 7 ± 12 days later than predicted).

[24] While precipitation and NDVI in the Okavango Delta showed a strong correlation to these measures in the Makgadikgadi, greater discrepancies occurred during extremely dry years. Precipitation in the Delta consistently underestimated NDVI in the grasslands in 2000–2001 (Figure 4), when rainfall rates at the start of the rainy season were exceptionally low in the Delta and, for the only time in the past decade, were exceeded by those in the Makgadikgadi grasslands. Conversely, during the rainy season of 2002–2003, the driest of the decade in the Makgadikgadi, the rainfall-based model consistently overestimated NDVI (Figure 4) due to the large disparity between rainfall in the two regions: the Delta received 50% more precipitation than the Makgadikgadi, compared to an average difference of $29 \pm 25\%$.

3.2. Movement Models

[25] Our simplest model explained 68% of variance in zebra locations along the migratory axis despite fixing the onset of migration at a single date and assuming constant speed (Table 1). However, environmentally dependent agent-based movement models (models 5–11) consistently outperformed the environmentally invariant models (models 1 and 3), with $R^2 > 0.9$ and $R^2 < 0.7$, respectively. Observed onset of migration showed a 10 day range (27 October to 5 November) and was best predicted by a weekly cumulative rainfall threshold set at $2.5 \, \text{mm}$ (a_1 in Table 1). The environmentally dependent agent-based models (models 5–11) all performed better when estimating date of departure from this rainfall threshold than from calendar day. The simpler models, which assumed environmentally invariant movement speeds once migration had started, generally performed less well but performed better when departure was predicted from calendar date rather than from rainfall rates (models 1 and 3 outperformed models 2 and 4).

[26] The most justified model to predict zebra movement (model 10) had four parameters, two linear functions of precipitation and NDVI, and a departure date model as a function of cumulative precipitation. It described a positive dependence on NDVI, i.e., zebras moved more slowly toward the Makgadikgadi (defined as a negative movement) when NDVI was high, and a negative dependence on precipitation, i.e., movement toward the Makgadikgadi was faster with higher precipitation. A more complex five-parameter model (model 11), with an interaction term between precipitation and NDVI, had a marginally higher R^2 (<0.01), but AIC analysis showed that this was not justified. Simpler dynamic models including only a linear (three parameters, model 5) or quadratic (four parameters, model 9) dependence on NVDI had very high prediction accuracy (0.903 and 0.907, respectively), indicating that NDVI alone can predict most of the variation in zebra movements.

4. Discussion

[27] As the majority of zebras in the Okavango Delta do not migrate, it seems unlikely that seasonal resource limitation drives the migration. Instead, the migratory animals appear to optimize their nutrition by moving to the Makgadikgadi grasslands during the rainy season when water is temporarily available in an area dominated by grasses with high protein and mineral content [*Brooks*, 2005]. Despite the low sample size, the high goodness of fit and statistical significance of our results show that the response to environmental conditions is highly robust, with low intrinsic variability among individuals, and so we are confident that the ability to tune migration activity to environmental variability is present in the population.

[28] We have shown that movement models driven by spatiotemporal environmental data can reveal decision rules, speed of movement, and navigation mechanisms employed by migratory animals [*Nathan et al.*, 2008; *Schick et al.*, 2008]. Overall, the movement models'

predictions corresponded very well with observations; indeed, they explained more than 90% of the zebras' movements toward their wet season habitat. While considerable variation in zebra movements toward the Makgadikgadi grasslands could be explained by calendar date alone, including satellite data on spatiotemporal environmental variability in the animals' surroundings identified environmental controls on the start and pace of migration. The zebras' departure from the Okavango Delta was not governed by an internal clock: Precipitation in the Okavango Delta held higher predictive power for the vegetation greenness in the Makgadikgadi than a fixed time of year, which explains the zebras' reliance on precipitation as a migration timing cue [*Geremia et al.*, 2011; *Olson et al.*, 2009].

[29] The best performing model estimated daily zebra movements from both NDVI and precipitation, indicating that they contain complementary information about the animals' migratory behavior. Recently, using data from arctic migrations, *Bischof et al.* [2012] suggested that migrating ungulates can either "surf" the wave of changing NDVI by moving in a way that follows the rate of change of NDVI or "jump" to the destination ahead of time and wait there until it reaches maximal conditions. The zebra movements we recorded indicate a combination of both strategies. After initiating migration, the zebras "surfed" in low-intermediate values of NDVI ahead of the peak greenness (Figure 2). However, the two most justified models predicted faster migratory movements when NDVI was low and rainfall was high, i.e., zebras travel faster later in migration (between km 100 and 0) when rains were more sustained, indicating that under these conditions, they prefer to jump ahead and reach the final destination ahead of peak NDVI. While the lacustrine soils of the Makgadikgadi support grasses with high nutritional value [*Baillieul*, 1979; *Brooks*, 2005], phytomass and consequently NDVI values are comparatively low throughout the rainy season. Therefore, in situ forage quality cannot account for the NDVI's predictive effect on zebra movements. Rather, it appears that together with rainfall, the gross photosynthesis of the landscape provides an integrated proxy of the zebras' expectation of forage and particularly water availability further along the migratory route. Thus, the zebras minimize the likelihood of encountering insufficient water and resources upon arrival in the Makgadikgadi by optimizing the prediction of conditions at their destination based on temporally correlated cues at the point of departure.

[30] We documented the reversal of migratory movements both to and from the Makgadikgadi grasslands under unusual environmental conditions. Similar behavior has been documented in blue wildebeest (*Connochaetes taurinus*) [e.g., *Maddock*, 1979; *Pennycuick*, 1975] and demonstrates the flexibility of ungulates when faced with decreased environmental predictability. This also suggests that zebras are facultative migrants that can rapidly occupy new areas through nomadic behavior. Annual rainfall has historically been highly variable in southern Africa [*Batisani and Yarnal*, 2010; *Mason and Jury*, 1997], and many climate change models predict that this variability will increase, and total rainfall decrease, during the 21st century [*Hulme et al.*, 2001].

[31] However, while the zebras adapt and, when necessary, reverse their migratory movements in response to environmental conditions, the cost of migrating is high and the benefits of an alternative seasonal range need to be weighed against the cost of migrating [*Bernstein et al.*, 1991; *Fryxell and Sinclair*, 1988]. Zebras need to graze 13 to 17 h per day to maintain condition [*Duncan*, 1992]. This would have been impossible during the migrations we recorded due to the distances traveled each day [*Bartlam-Brooks et al.*, 2011], so the Okavango-Makgadikgadi migration is energetically costly and compromises overall body condition. Under climate change scenarios of reduced total rainfall and increased rainfall variability at the start of the rainy season, the cost of failed migrations may eventually outweigh the benefit of spending the rainy season in the Makgadikgadi grasslands.

[32] Nonetheless, the facultative nature of the migration, the zebras' rapid adjustments to environmental conditions and their ability to reverse migration to avoid adverse conditions or exploit renewed resource availability, indicates a degree of resilience to environmental change. Understanding the cues that drive long-distance animal movements is critical to predicting the fate of migrations under different environmental change scenarios. Continued monitoring of the migration, and the environmental conditions that influence it, will reveal whether the animals learn to prevent failed migrations by adjusting the environmental cues they rely on and culturally transmit such new migration strategies. Since increasing density dependence during the season when parts of the population can potentially migrate (nonshared season) widens the range of migration-survival values where partial migration is expected to occur [*Taylor and Norris*, 2007], changes in zebra population density in the Okavango may also affect the number of migrating individuals.

5. Conclusions and Implications

[33] We have shown that combining time series of freely available environmental satellite images with animal tracking data to develop predictive migration models is a powerful and cost-effective tool to visualize and study how landscape-scale animal movement behavior is influenced by spatiotemporal changes in the environment. This is of great applied value: The ability to forecast movement and habitat use by migratory animals over daily to weekly time steps, and with the accuracy demonstrated here, can inform conservation strategies in near real time. Recent developments of Movebank, a free online animal movement archive (www.movebank.org) [*Kranstauber et al.*, 2011], now allow the automated annotation of movement tracks with a large array of remote sensing, weather, and other geographic data sources [*Dodge et al.*, 2013]. Unlike methods that cover only the temporal or spatial dimension [*Tomkiewicz et al.*, 2010], movement models driven by spatiotemporal environmental data can help reveal decision rules, orientation, and navigation mechanisms employed in migration. In addition, they can ultimately also shed light on slower processes, such as the effects of environmental heterogeneity on population densities, which are poorly understood in migratory species [*Hebblewhite and Haydon*, 2010; *Singh and Milner-Gulland*, 2011].

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