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Opposing Rainfall and Plant Nutritional Gradients Best Explain the Wildebeest Migration in the Serengeti

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abstract: Multiple hypotheses have been proposed to explain the annual migration of the Serengeti wildebeest, but few studies have compared distribution patterns with environmental drivers. We used a rainfall-driven model of grass dynamics and wildebeest movement to generate simulated monthly wildebeest distributions, with wildebeest movement decisions depending on 14 candidate models of adaptive movement in response to resource availability. We used information-theoretic approaches to compare the fits of simulated and observed monthly distribution patterns at two spatial scales over a 3-year period. Models that included the intake rate and nitrogen (N) concentration of green grass and the suppressive effect of tree cover on grass biomass provided the best model fits at both spatial scales tested, suggesting that digestive constraints and protein requirements may play key roles in driving migratory behavior. The emergence of a migration was predicted to be dependent on the ability of the wildebeest to track changes in resource abundance at relatively large scales (>80–100 km). When movement decisions are based solely on local resource availability, the wildebeest fail to migrate across the ecosystem. Our study highlights the potentially key role of strong and countervailing seasonally driven rainfall and fertility gradients—a consistent feature of African savanna ecosystems—as drivers of long-distance seasonal migrations in ungulates.

Keywords: Connochaetes taurinus, dynamic model fitting, emergent behaviors, resource landscapes, spatial autocorrelation.

Introduction

Long-distance ungulate migrations constitute one of the great spectacles of nature and have been documented across a wide range of ecosystems (Craighead et al. 1972; Fryxell and Sinclair 1988; Williamson et al. 1988; Fancy et al. 1989; Berger 2004). By moving seasonally between geographic locations that differ in terms of food intake, survival, and fecundity, many species have evolved an effective life-history strategy for exploiting heterogeneous

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environments (Fryxell et al. 1988; Berger 2004). The wildebeest (*Connochaetes taurinus*) migration in the Serengeti/Mara ecosystem of Tanzania and Kenya represents an iconic example of ungulate migration and constitutes one of the most thoroughly documented animal migrations in one of the most intensively studied ecosystems on Earth (Pennycuick 1975; Maddock 1979; Fryxell et al. 1988; Mduma et al. 1999; Wilmshurst et al. 1999*b*; Wolanski and Gereta 2001; Sinclair 2003; Musiega and Kazadi 2004; Boone et al. 2006). Surprisingly, however, we still lack a satisfactory mechanistic explanation of the Serengeti migration. The Serengeti wildebeest, by virtue of their large numbers, are widely regarded as ecosystem engineers (Sinclair 1979, 2003; Holdo et al. 2007), so understanding exactly which variables determine their migratory patterns and how these might evolve over time (e.g., as a result of global climate change) becomes of particular importance.

In the Serengeti migration, up to 1.4 million wildebeest, plus large numbers of zebra (*Equus burchelli*) and Thomson's gazelles (*Gazella thomsoni*), move seasonally between dry and wet season ranges over a 30,000-km² area. It is clear that this migration is ultimately driven by the marked and strongly seasonal rainfall gradient that runs from the southeastern short-grass plains to the tall-grass woodland and savanna habitats in the north, center, and west of the ecosystem (Pennycuick 1975; McNaughton 1979*a*; Sinclair 1979; Boone et al. 2006). This gradient imposes a constraint: at the end of the wet season, migrant species leave the plains as the latter dry up and green grass and surface water become confined to the wetter, northern reaches of the ecosystem (McNaughton 1979*a*). These constraints compel wildebeest and other migratory species to move north. What is less clear is what the proximate factors are that drive the wildebeest into the plains at the onset of the wet season to begin with, since rainfall (the main determinant of forage production) is higher in the woodlands than in the plains throughout the year. Several explanations have been postulated to explain this movement onto the plains, including higher forage abundance and quality,

surface water nutrient content, and escape from predation (Jarman and Sinclair 1979; Fryxell et al. 1988; Murray 1995; Wolanski and Gereta 2001). So far, however, few studies have systematically tested any of these hypotheses by confronting wildebeest movement models with data.

Recently, Wilmshurst et al. (1999a) showed that wildebeest show a significant preference for grass patches of short to medium height at the landscape scale. Because energy intake shows a hump-shaped response as a function of grass height (Wilmshurst et al. 1999b, 2000), wildebeest movement patterns follow an energy maximization strategy, a finding supported at a more restricted spatial scale for Thomson's gazelles, another migratory species (Fryxell et al. 2004). Also in a recent article, Boone et al. (2006) used evolutionary programming (EP) to show that simulated wildebeest evolve migratory pathways that resemble those observed in nature when moving across a landscape containing information on rainfall and the normalized difference vegetation index (NDVI), an index of plant productivity, suggesting that seasonal fluctuations in primary productivity can account for the migration (Boone et al. 2006). A potential difficulty with the analysis of Boone et al. (2006), however, is that the wildebeest in the EP model evolve to move toward areas that experience high rates of change in NDVI in the plains during the wet season, but these are also areas of lower absolute NDVI and, by inference, lower peak green biomass than the woodlands. Boone et al. (2006) suggest that changes in NDVI measure new forage production, but it could be argued that these changes track (rather than explain) wildebeest grazing patterns, given that wildebeest grazing can more than double grass primary production in the Serengeti plains (McNaughton 1985). In addition, NDVI generally does not distinguish between woody and herbaceous green biomass (Lu et al. 2003; Boone et al. 2006), so it quantifies different resources in the treeless plains and the woodlands, which consist of a tree-grass mixture (Sinclair 1979). Wildebeest in the EP model also move toward areas of high relative rainfall (measured as monthly rain expressed as a proportion of the annual total), even though absolute rainfall has been shown to be the best predictor of primary production in the Serengeti (Sinclair 1975; McNaughton 1985). These derived variables allow the EP model to generate a reasonable approximation to the migration, but they do not necessarily pinpoint the resources that drive the migration and movement in general across the landscape.

Like Boone et al. (2006), in this article we focus primarily on forage availability as the main driver of wildebeest spatial distribution patterns, but we expand on their approach by teasing apart the effects of forage quality and nutrient content, tree-grass competition, and abiotic factors such as terrain characteristics and water availability on habitat selection and assume that movement decisions respond to seasonally fluctuating environmental conditions. Following Wilmshurst et al. (1999a), we incorporate realistic functional responses and digestive constraints into a mechanistic model of food intake. We fit a series of competing models for wildebeest movement driven by environmental variables to wildebeest distribution data, using geostatistical methods to allow the data to identify the model providing the best fit to the observed distribution patterns. Finally, we use our model to conduct a theoretical investigation of the spatial scale of resource tracking used by wildebeest, as reflected by the size of local movement neighborhoods, to infer the minimum conditions under which migration can occur within an adaptive movement framework. We believe the approach we take here provides a useful linkage among herbivore foraging decisions, landscape patterns, competitive interactions, and emergent spatial distributions.

Material and Methods

Study System

The Serengeti ecosystem (fig. 1) can be broadly divided into two main habitat types: the treeless, short-grass plains
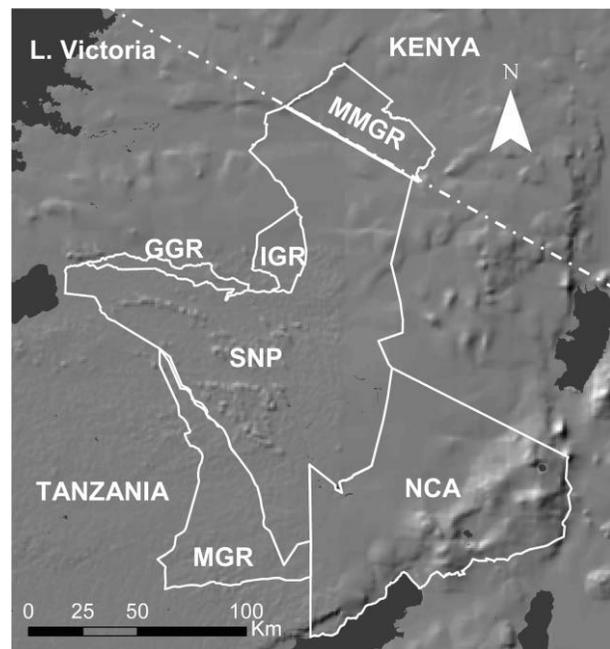

Figure 1: Map of the Serengeti ecosystem showing key protected areas and geographic features (water bodies are shown in dark gray, and topographical features in lighter shades of gray). SNP = Serengeti National Park, NCA = Ngorongoro Conservation Area, $MMGR$ = Masai Mara Game Reserve (GR), MGR = Maswa GR, IGR = Ikorongo GR, and GGR = Grumeti GR.

in the southeastern portion of the ecosystem ("plains" hereafter) and the tall-grass savanna and woodland ("woodlands") in the north and west (fig. 2*B*). Wildebeest are the dominant herbivores in this system, with a population that has fluctuated between 1 and 1.4 million animals over the past quarter-century. The Serengeti is characterized by strong climatic and edaphic gradients and discontinuities. A marked precipitation gradient runs in a southeast to northwest direction, ranging from less than 400 mm in the rain shadow of the Ngorongoro volcano to more than 1,200 mm near the shores of Lake Victoria (fig. 1). In addition to this gradient, there is substantial regional heterogeneity in soil properties. The plains soils are shallow, nutrient-rich volcanic ashes with an almost continuous hardpan layer that impedes tree growth (Sinclair 1979). In the north, soils tend to be dystrophic, with a lower clay content than in the plains (Sinclair 1979). For the purposes of our analysis, the Serengeti ecosystem is regarded as the area bounded by the wildebeest migration, as defined by Maddock (1979), covering a surface area of 30,700 km² (fig. 1).

Approach and Data Sources

A basic assumption of our model is that wildebeest movements track real-time environmental conditions and resource availability and that we can use observed distributions against the template of alternative resources to make inferences about movement rules. The resources and environmental drivers we included here as candidates for informing movement decisions are forage biomass, intake, and quality; water availability; and tree cover (which affects forage biomass). We focused on plant nitrogen (N) and sodium (Na) as key indicators of forage quality because of the importance previously attached to crude protein and Na for Serengeti herbivores (Sinclair 1977; McNaughton 1988; Murray 1995). We also included an index of topographic roughness as a covariate, because this may influence access to resources. To find the combination of environmental drivers that best predict wildebeest distribution patterns, we fit a wildebeest movement model to detailed monthly wildebeest distribution data spanning a 3-year period over the entire Serengeti.

The main data set underpinning our analysis is a set of monthly distribution maps of the Serengeti wildebeest population based on monthly aerial surveys conducted between August 1969 and August 1972, known as the "recce" data (Norton-Griffiths 1973; Maddock 1979; Boone et al. 2006). To this date, the recce data constitute the only time series showing seasonal shifts in the spatial distribution of the entire wildebeest herd in the Serengeti and thus the only comprehensive data source detailed enough to analyze the migration at the population level. Given the importance attributed to the migration, it is surprising both that such data have not been collected since and that the recce data have not been analyzed in greater detail.

The collection of the wildebeest recce data has been described in detail elsewhere (Norton-Griffiths 1973; Maddock 1979). For this study, we adopted two spatial scales:
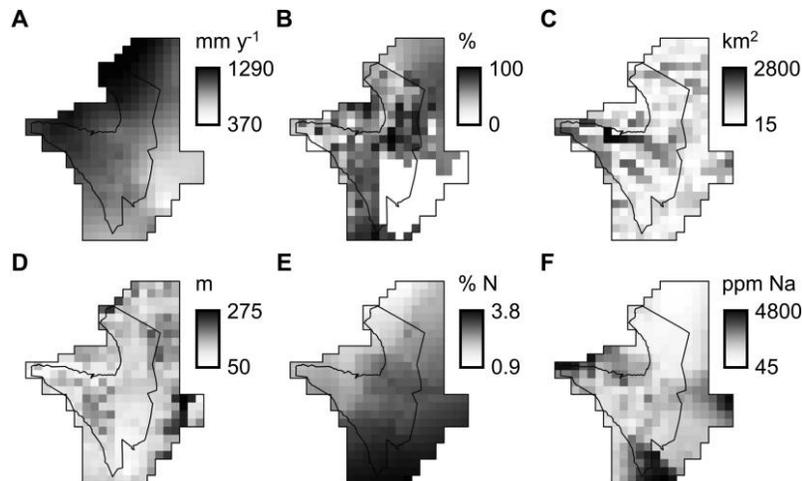

Figure 2: Environmental variables used to model wildebeest distribution patterns in the Serengeti ecosystem (defined by the extent of the wildebeest migration), shown at 10-km resolution. *A*, Rainfall (varies monthly in the model; shown here as 1969–1972 annual mean); *B*, Percent tree cover; *C*, Flow accumulation (shown here unweighted by rainfall) in km²; *D*, Terrain roughness, expressed as the standard deviation of elevation across 100 1-km² pixels, *E*, Plant N concentration; and *F*, Plant Na concentration. The total area covered represents 30,700 km². The boundary of Serengeti National Park is shown inset for reference.

the fine-scale resolution (10 km) used by Maddock (1979) and a coarse-scale (25 km) resolution. We conducted the analysis at the coarse resolution (25 km) to examine whether misregistration of spatial information might lead to erroneous rejection of particular models at the finer scale. Misregistration occurs when two maps show similar spatial patterns but do not "line up" (Costanza 1989), and it occurs more frequently at finer spatial scales. Details on the development of wildebeest distribution maps and the geographical information system (GIS) layers of the environmental drivers are given in appendix A in the online edition of the *American Naturalist.*

Wildebeest Movement Model

The wildebeest movement model is a discrete-time, spatially explicit simulation model of grass and wildebeest dynamics. The model is implemented across a lattice following the boundaries of the ecosystem as defined by the recce data (fig. 2), at both fine (10 km) and coarse (25 km) resolutions. Both within-cell daily dynamics—grass growth and decay (determined by monthly rainfall) and herbivory—and between-cell weekly dynamics—wildebeest movement—occur in the model, which is described in detail by Holdo et al. (2009) and summarized in appendix B in the online edition of the *American Naturalist.* The model generates maps of wildebeest distribution patterns, which can then be compared to observed distribution patterns. Wildebeest emigration from a cell at each time step is governed by the value of a resource variable Z within the cell (Z_{ij}) in relation to its mean value evaluated within a surrounding neighborhood of radius r (Z_r) according to the equation

$$\Theta_{ij} = \frac{E(Z_r)^\varphi}{(Z_{ij})^\varphi + E(Z_r)^\varphi} W_{ij} \qquad (1)$$

(following Fryxell et al. 2004), where Θ_{ij} (see eq. [B9]) represents the emigration of wildebeest W_{ij} from cell ij, $E(Z_r)$ is the expected value of Z_r across the neighborhood, and φ controls the shape of the migration function. An increasingly strong dispersal response occurs as φ increases. The variable r represents a circle of radius r surrounding each cell, defined as the "resource tracking neighborhood." We assume that at any given time, wildebeest track resources across the landscape up to a distance r and then disperse within this local neighborhood. Wildebeest that emigrate from a cell distribute themselves proportionately throughout the subset of target cells within the resource tracking neighborhood that are of greater value than the cell they have left, as assumed by Fryxell et al. (2004). Wildebeest distributions are updated with a weekly rather than daily time step because of con-

straints imposed by the high computational burden of the movement submodel. We show later that using a daily time step does not alter our conclusions.

One of our primary objectives en route to developing a movement model was to find the functional form of Z that maximizes the fit between the model and the wildebeest distribution data. We selected 14 candidate models that differed in terms of the combination of variables defining Z: green grass biomass G and intake I, tree cover T (fig. 2*B*), surface water availability or flow accumulation F (fig. 2*C*), terrain roughness R (fig. 2*D*), and grass nitrogen N (fig. 2*E*) and sodium Na (fig. 2*F*) concentrations (table 1). Of these variables, some were directly obtainable from GIS layers of the ecosystem (fig. 2), whereas others (such as green grass biomass and intake) were derived variables generated by the movement model. We used the model $Z = G$ as a "null" or base model, given that green grass abundance is known to be one key driver of habitat choice in the Serengeti (McNaughton 1979*a*). The inclusion of green grass intake instead of green grass biomass in several models allowed digestive constraints on green grass intake imposed by the presence of dry grass biomass and digestive capacity limitations to be incorporated in the model. In several of the candidate models, we included either GN^β or IN^β as terms of Z (table 1). This allowed the simultaneous inclusion of the effects of grass biomass (or intake) and quality (in terms of nutrient concentration) in the resource function; the model with $Z = IN^\beta$ implies that wildebeest maximize intake of green grass multiplied by a power function of its N concentration. The use of the exponent β allowed relatively flexible (i.e., nonlinear) functional forms to be fitted without having to estimate a large number of parameters (cf. Pacala et al. 1994). It also allowed us to evaluate the comparative strength of grass biomass or intake versus grass nutrient concentration in informing movement decisions; for example, when $\beta > 1$, wildebeest will respond disproportionately to grass N in comparison to grass biomass. We also used power functions when testing the effects of flow accumulation and terrain roughness on habitat choice (table 1). To incorporate the effect of tree-grass competition, we also included the term $e^{-\omega T}$ in some of the models; for example, the model *I,T,N*, with $Z = Ie^{-\omega T}N^\beta$, includes intake, grass N, and suppressive effects of tree cover on the amount of area occupied by grass (table 1).

Fitting the Dynamic Model to Distribution Data

The dynamic model generated maps of predicted wildebeest abundance (Y) across the Serengeti at monthly intervals between August 1969 and August 1972. We used the 33 months that matched the survey flights from the recce data to obtain mean wildebeest abundances $Y_{\text{model, }ijs}$

Table 1: Candidate models and ordinary least squares (OLS) and autoregressive (AR) model fits for wildebeest movement models in the Serengeti ecosystem between 1969 and 1972

Variables in model	Z	p	ΔAIC$_C$[a] OLS 25 km	AR 25 km	OLS 10 km
G	G	0	226.8	126.3	638.6
G,T	$Ge^{-\omega T}$	1	123.9	117.2	548.5
G,N	GN^β	1	55.3	71.6	232.2
G,T,N	$Ge^{-\omega T}N^\beta$	2	44.3	56.5	107.5
I	I	0	103.1	58.1	283.0
I,T	$Ie^{-\omega T}$	1	72.4	72.2	162.8
I,N	IN^β	1	25.8	53.9	143.9
I,T,N	$Ie^{-\omega T}N^\beta$	2	21.9	48.0	.0
I,T,Na	$Ie^{-\omega T}(Na)^\beta$	2	78.0	80.9	107.5
I,T,N,Na	$Ie^{-\omega T}N^\beta + \gamma(Na)^\delta$	4	26.6	53.5	42.7
I,T,N,F	$Ie^{-\omega T}N^\beta + \gamma F^\delta$	4	.0	.0	.4
I,T,N,R	$Ie^{-\omega T}N^\beta + \gamma R^\delta$	4	12.2	46.3	4.1
I,N,F	$IN^\beta + \gamma F^\delta$	3	2.6	3.8	135.4
I,F	$I + \gamma F^\delta$	2	56.6	22.0	144.5

Note: Z refers to the resources or environmental covariates that drive movement across the landscape in each model (see eq. [1]). The quantity p (see eq. [2]) equals the number of movement model parameters (Greek letters in function Z; it excludes k, the number of autocorrelation function parameters). Variable definitions: G = green grass biomass; I = green grass intake; T = tree cover; N = grass N concentration; Na = grass Na concentration; F = flow accumulation; R = terrain roughness.

[a] Corrected Akaike Information Criterion value relative to best model.

(where i and j are cell coordinates and s is the season) for the three distinct annual seasons. We then compared these modeled abundances with the observed wildebeest abundances $Y_{obs, ijs}$. This is a regression problem in which either the original data or the fitted residuals can exhibit spatial and/or temporal autocorrelation, potentially leading to problems of inference and parameter bias (Haining 1990, pp. 40–41; Hoeting et al. 2006; Ives and Zhu 2006; Dormann 2007). Taking account of both spatial and temporal autocorrelation in this case would require computationally intensive Monte Carlo methods that are beyond the scope of this study (Ver Hoeff et al. 2001). We minimized the problem of temporal autocorrelation by using seasonal rather than monthly distributions, thereby sacrificing some information. We tested for spatial autocorrelation by computing Moran's I as a function of lag distance (Legendre and Legendre 1998, p. 714; Lichstein et al. 2002) for the fitted residuals after first fitting the model to data using ordinary least squares (OLS) methods, and we then repeated the analysis using an autoregressive (AR) approach. We assumed a lognormal distribution for wildebeest abundances because this transformation improved the distributional properties of the data and the residuals. Our procedure for calculating OLS and AR likelihoods is given in appendix C in the online edition of the *American Naturalist.*

Following the estimation of the log likelihoods for each model, we used a modified version of the corrected Akaike Information Criterion (AIC$_c$) to compare the goodness of fit of competing models (Hoeting et al. 2006):

$$\text{AIC}_c = -2\ell + 2ns\frac{p + k + 1}{ns - p - k - 2}, \qquad (2)$$

where ℓ is the log likelihood, n is the number of cells in the lattice, s is the number of seasons (and thus ns gives the total number of observations), p is the number of parameters fit to the movement model, and k is the number of parameters associated with the autocorrelation functions, equal to 0 in the OLS models.

To test the robustness of our model fits to uncertainty in the environmental data layers and model parameters, we conducted an error analysis by running all of the models with alternative realizations of the input GIS layers and some key parameters (Pacala et al. 1996; Holdo 2007). In particular, many of our environmental covariates (as interpolated maps) were generated from observations collected at a limited number of sites, and there was, therefore, considerable uncertainty associated with undersampled regions; this uncertainty can propagate through the model (Kyriakidis 2001). To keep the error analysis manageable, we focused the analysis on those layers and parameters that were most likely to draw contrasts between alternative models. For example, rainfall-driven grass

growth is common to all models, so we kept the monthly rainfall layers and grass growth parameters at their default values. Of primary interest to us were the effects of plant nutrients, tree cover, surface water, and intake versus biomass as explanatory factors in the migration, so we incorporated uncertainty in plant N and Na, tree cover T, and four dynamic model parameters associated with intake rates (α_w, β_w, and daily voluntary intakes DVI_G and DVI_D, described in app. B) in the error analysis. We did not model uncertainty in flow accumulation because of the large computational burden associated with producing these monthly maps. For each of 1,000 random realizations of these input maps and parameters, we fit all 14 models to the data and computed AIC_c values. We used the 25-km resolution and OLS because of the prohibitive computational burden imposed by using either the AR approach or the OLS analysis at 10-km resolution. The resampling procedure we used to generate input maps and parameters is outlined in appendix D in the online edition of the *American Naturalist*.

Finally, to compare the performance of our model to that of the only other model of the wildebeest migration produced to date (the EP model of Boone et al. 2006), we refit our best overall 10-km model at the higher 5-km resolution used in EP. Although our model-fitting procedure (see below) differed from that used by Boone et al. (2006), we used their classification system to compare model fits. In the EP model, the raw census data (see app. A) were used to produce a binary classification of lattice cells as occupied ($\geq$250 animals) or unoccupied ($<$250 animals). Unlike our seasonal approach, 12 monthly distribution maps averaged over the entire census period (1969–1972) were produced and compared with the maps generated by the model. An index of fit is provided by the mean number of cells (averaged across all months) that are occupied in both model and data as a fraction of the total number of cells occupied in either model or data.

In addition to testing model fits with AIC_c, we conducted a graphical comparison of the ability of competing models to generate a migration. We defined the term "migration distance" (d_m) as the distance between the centroids of the entire wildebeest herd averaged through the wet and dry seasons (defined as the December–April and August–November seasons). We calculated the migration distance for the actual wildebeest distribution (the observed value of d_m) and for each of the candidate models. We then graphically compared the observed and modeled values of d_m.

Resource Tracking Neighborhood

The default scenario in the model comparison is to assume that wildebeest can track resources and disperse over a

radius $r \rightarrow \infty$; that is, wildebeest can make movement decisions based on the entire landscape and are therefore "omniscient." To investigate how migration and overall model fit are affected by the size of the resource-tracking neighborhood, we refit the best overall candidate model to the data with fixed values of r ranging between 10 km (a neighborhood that would include only adjacent cells) and 200 km and plotted d_m and the log likelihood profile as functions of r.

Results

OLS Model Fits

In the OLS analysis, different models provided the best fits to the data at 10- and 25-km resolutions. At the coarse resolution, the model with the lowest AIC_C value (and therefore the best fit) included terms for intake, tree cover, plant N, and flow accumulation (model I,T,N,F), whereas at the fine resolution, model I,T,N (intake, tree cover, and plant N) provided the best overall fit (table 1; video 1). In both cases, green biomass intake I was a better predictor of wildebeest distribution patterns than green biomass G, and the inclusion of plant N in the function Z improved fit over simpler models (table 1). Although the inclusion of tree cover did improve model fit at the 25-km resolution over simpler models when flow accumulation (F) was excluded from the analysis, this covariate provided a marginal improvement to model fit only when water availability was taken into account at this scale (table 1). At the 10-km resolution, tree cover greatly improved fit over simpler models, and flow accumulation had little explan-
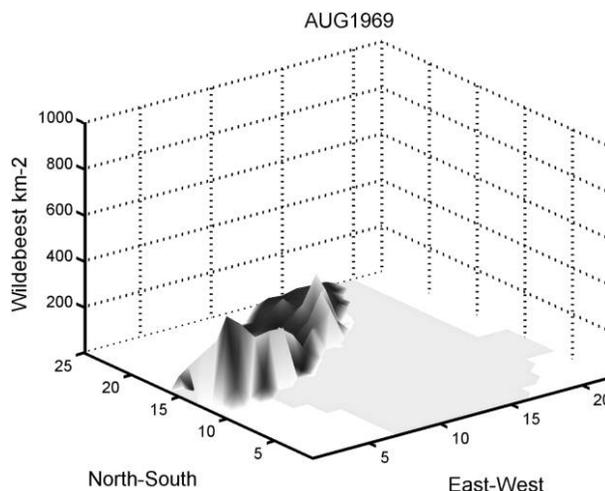
Video 1: Representation of movement model I,T,N at fine scale. Figure is the initial frame from a movie of the simulated migration, which is available in the online edition of the *American Naturalist*.

atory power (table 1). At both spatial resolutions, neither plant Na nor terrain roughness R improved model fits.

The error analysis strongly supported the conclusions of the analysis conducted with the default layers and parameters (table D1). In most cases (particularly for the best models), model ranks obtained in the default case were preserved when error in the environmental layers and parameters was included. In addition to generating confidence limits for our AIC_C values, we compared the rank of any given model with the rank of the next-best model for each realization of the error analysis, and we found that our model rankings had very strong support (table D1). For example, the inclusion of tree cover and nitrogen consistently improved model fit, and intake models strongly outperformed biomass models (table D1). To test whether surface water and tree cover may be somewhat confounded with each other, we examined the bivariate correlations between these and other input layers (table E1 in the online edition of the *American Naturalist*). Generally, the correlations among the environmental variables were weak, including that between tree cover and flow accumulation. The only notable relationships were between plant N and Na, which showed a moderate positive correlation, and plant N and rainfall, which were quite strongly negatively correlated (table E1).

An examination of the maximum likelihood estimates (MLEs) for the dynamic model parameters (table 2) showed that variation in plant N concentration across the landscape (fig. 2*E*) is more influential than tree cover (fig. 2*B*) or water availability (fig. 2*C*) in affecting wildebeest distribution patterns in the model. An approximate indication of the influence of a particular variable is given by comparing the ratio of Z with the variable in question set at its maximum and minimum values (with parameters set to their MLEs) across the ecosystem. This ratio can then be compared across variables. Using this approach,

the estimated value of β, the power term in the function $Z = Ie^{-\omega T}N^{\beta}$, suggests a 40-fold difference in the "attractiveness" of areas with the lowest and highest plant N content, whereas the estimated value of ω (which controls the effect of tree cover on grass biomass) produces a ratio about half as large (see table 2 for parameter estimates). Similarly, the estimated values of parameters γ and δ, which determine the influence of flow accumulation on habitat choice (table 2), result in a twofold variation in the value of this term in the resource function Z (table 2). The multivariate confidence bounds for each of the parameters estimated, drawn from the Metropolis sampling distributions, are shown in figure E2. In addition to showing confidence bounds, these plots indicate relationships among the parameters. Figure E2*A* and E2*B* shows that the coefficient γ and exponent δ for the flow accumulation term F (where $Z = IN^{\beta} + \gamma F^{\delta}$; see table 2) in the I,N,F model appear to be strongly correlated, but neither of these parameters is correlated with the β exponent of the nitrogen term N. This suggests that a simpler model lacking a δ parameter (i.e., $\delta = 1$) would have provided an equally good fit, but it also suggests that the contributions of N and F in the model are independent and not confounded. Figure E2*D* also suggests that the effects of tree cover (parameter ω) and N (parameter β) are independent, which was to be expected given the weak correlation between these two environmental covariates across the landscape.

In terms of migration distance (d_m), some models were far more successful in generating a seasonal migration than others (fig. 3*A*). The simplest model (G) performed particularly poorly, and replacing green biomass with green biomass intake (I) substantially lengthened the migration distance generated by the model (fig. 2*A*). Generally, models that included a plant N term resulted in migration

Table 2: Maximum likelihood estimates (MLEs) and multivariate 95% confidence intervals (lower and upper bounds) for best-fit model parameters

Model	Z	Lattice (km)	Parameter[a]	MLE	Lower	Upper
I,N,F (OLS)	$IN^{\beta} + \gamma F^{\delta}$	25	β	3.34	2.20	4.99
			γ	9.50	1.49	99.94
			δ	.34	.01	1.30
I,N,F (AR)	$IN^{\beta} + \gamma F^{\delta}$	25	β	3.09	1.62	4.31
			γ	32.14	.82	99.93
			δ	.50	.11	1.39
			θ_1[b]	1.94	1.26	4.73
			θ_2[b]	1.39	.57	4.97
I,T,N (OLS)	$Ie^{-\omega T}N^{\beta}$	10	ω	.031	.026	.033
			β	2.99	2.76	3.50

[a] See table 1 for a list of parameters.

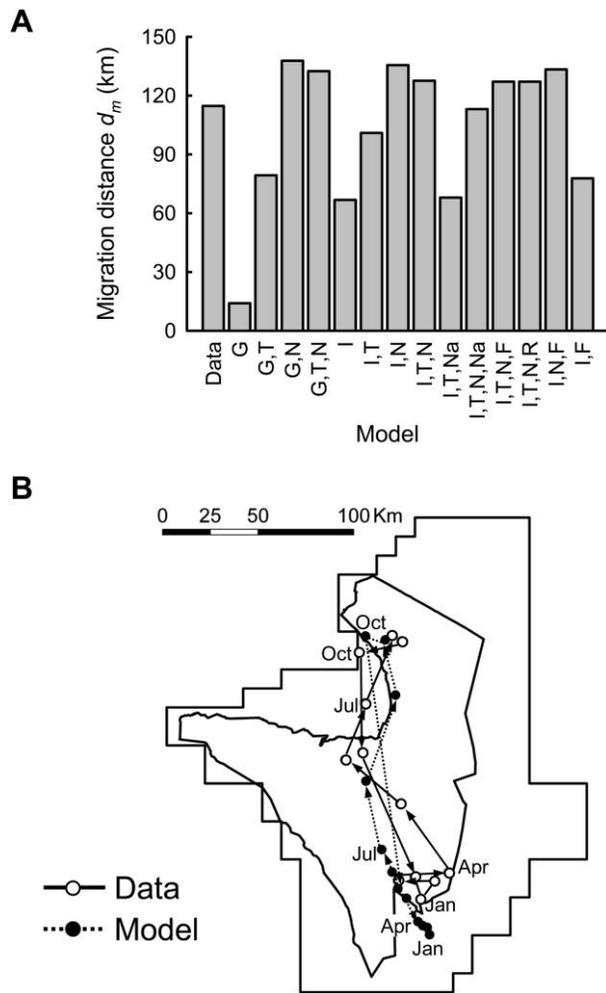[b] Parameter in the AR likelihood function (see app. C in the online edition of the *American Naturalist*).

A

B

Figure 3: *A*, Observed and modeled migration distance d_m of the wildebeest herd, defined as the distance between the centroids of the herd averaged separately for the wet (December–April) and dry (August–November) seasons. The seasonal values are means computed over the period August 1969–August 1972. The observed value is compared with that of 14 candidate models, identified by the environmental variables that they include (see table 1 for model descriptions). *B*, Observed and simulated (based on the best movement model *I,T,N*, which incorporates green grass intake, grass N content, and tree cover) monthly locations of the "center of mass" of the Serengeti wildebeest population averaged over the 1969–1972 time period.

distances that most closely match the value of d_m calculated from the data (fig. 3*A*).

The predicted seasonal wildebeest distributions for the best 10-km resolution OLS model (*I,T,N*) are shown alongside the observed distributions in figures 3*B* and 4. The fits between model and data were best at the extremes of the migration (December–April and August–November) and poorer during the transition period (May–July). During this transition period, wildebeest tend to move

toward the central woodlands and western corridor of the Serengeti. Even in the best model, wildebeest tend to persist in the southern portion of the ecosystem during this period (figs. 3*B*, 4).

AR Model Fits

Since significant spatial autocorrelation was detected in model residuals in even the best-fitting models for both the 10- and 25-km resolutions (fig. E1), we used an autoregressive approach in addition to the OLS analysis. As outlined in appendix C, we used an iterative procedure to estimate the model and covariance function parameters. At the fine resolution, this convergence was unsuccessful for several of the candidate models, especially those providing poor fits in the OLS analysis, so we report results only at 25-km resolution. The autoregressive approach identified the same model (*I,T,N,F*) that provided the best fit in the OLS case (table 1), suggesting that even after correcting for the effects of spatial autocorrelation the same variables emerge as the drivers of the wildebeest migration and distribution patterns. The MLE for the autocorrelation distance parameter (θ_1 in app. C) was of the order of 50 km (table 2; fig. E2).

Resource-Tracking Neighborhood

When the best overall model was run with different resource tracking neighborhood radii (r), we found that model fit, in terms of both model likelihood and migration distance, improved monotonically up to a distance of 80–100 km, with no appreciable improvement in fit for larger neighborhoods (fig. 5). This implies that wildebeest in the dynamic model need to be able to track landscape conditions over relatively large distances in order to replicate the movement patterns that are actually observed. The plot of migration distance in particular (fig. 5*B*) suggested that when wildebeest move only within local neighborhoods (<80 km), there is little or no emergent pattern of long-distance movement, and the simulated population tends to get "trapped" within certain portions of the landscape. To test whether this effect was an artifact of our weekly movement iteration or our choice of spatial scale, we repeated the simulation (i) with a daily movement step and (ii) at a spatial resolution of 5 km and had similar results in both cases (fig. 5*A*), suggesting that the perception radius threshold effect is not generated by the model structure or choice of spatial resolution but rather reflects the spatial scale of seasonal environmental change and how it needs to be tracked to be exploited effectively. Note that although wildebeest are unlikely to be able to move across the entire landscape in a single day (the maximum daily distance recorded in the literature is 50 km; Talbot and
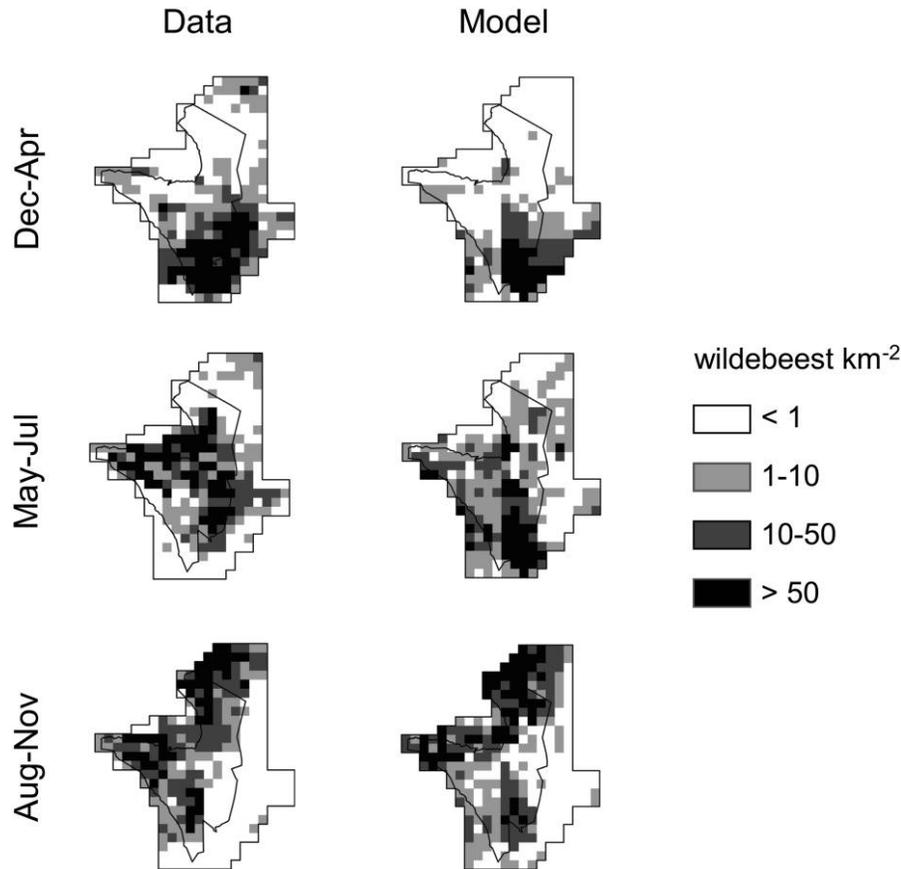
Figure 4: Observed wildebeest distribution patterns (individuals km^{-2}) in the Serengeti ecosystem versus modeled output from the best-fit ordinary least squares simulation model (I,T,N) at 10-km resolution. The distributions (both actual and modeled) represent seasonal means derived from monthly layers spanning the period August 1969–August 1972.

Talbot 1963), our results show that increasing the frequency of movements in our model without increasing the size of the perception window does not increase the ability of modeled wildebeest to track environmental gradients efficiently enough to allow long-distance migration.

Discussion

Grass Intake and Nutritional Quality Explain the Migration

Our model suggests that green grass intake and protein content both play a key role in determining the movement and distribution patterns of migratory wildebeest in the Serengeti. Green grass intake is a much better predictor of the wildebeest migration than is grass biomass, and maximizing this quantity rather than biomass helps to explain not only local movement patterns but also long-distance migration.

Previous studies on both wildebeest and Thomson's ga-

zelle movements in the Serengeti suggested that ungulates follow energy-maximizing rather than simply biomass-maximizing strategies (Wilmshurst et al. 1999*a*; Fryxell et al. 2004). Because the quality of grasses (as measured by protein, fiber, and/or energy content) generally declines and intake increases as a function of grass height or biomass, energy intake is often optimized in areas of intermediate grass height or biomass (Wilmshurst et al. 1999*a*; Fryxell et al. 2004). Although a single variable (biomass) may in some cases suffice to model both quantity and quality of forage intake (Fryxell et al. 2004), here we partitioned grasses into high- and low-quality (green and dry grass, respectively) compartments. This allowed us to treat food quantity and quality independently, which can be important in distinguishing between growing and senescing swards that may have equal biomass but differ in quality. Despite differences in model details, however, our conclusions are consistent with the previous finding (Wilmshurst et al. 1999*a*) that what is being optimized by the wildebeest is
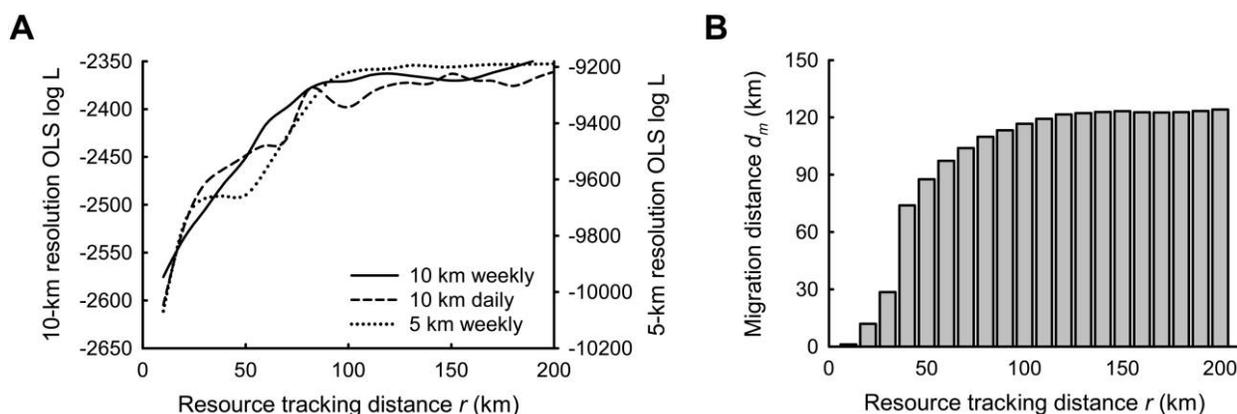
Figure 5: *A*, Ordinary least squares likelihood profile (assuming weekly and daily movement intervals at 10-km resolution and weekly movement at 5-km resolution), and *B*, migration distance d_m (assuming weekly movement at 10-km resolution, the model default) for the best overall model (*I*,*T*,*N*) as a function of the radius of the resource tracking neighborhood in the simulation model.

the rate of intake of the high-quality compartment. This intake rate is not simply a monotonic function of biomass, because (i) new green grass growth is inhibited by the accumulation over time of dry grass due to senescence, and (ii) digestive constraints on intake are imposed by the inevitable consumption of some dry grass in a green-dry grass mixture. This means that as the season progresses, areas with abundant dry grass will tend to be avoided because they reduce green grass intake. Green grass intake thus follows an approximately unimodal relationship with total grass biomass and may serve as a proxy for energy intake.

An added aspect of food quality that we explicitly considered is grass crude protein or N concentration. Whereas the intake variable incorporates a seasonally varying component of food quality (in addition to quantity), our use of landscape-level variation in plant N (or protein) content adds an additional spatial component that is fixed over time. This plant N gradient is strongly correlated with a soil N gradient (McNaughton 1985; Ruess and Seagle 1994) that is opposite of the rainfall gradient in the Serengeti: the nutrient-rich plains of the southeastern portion of the Serengeti lie on volcanic soils and are at the low end of the rainfall spectrum, whereas the sandier woodland soils of the central and northern Serengeti receive more rainfall but are less fertile (Sinclair 1979). Our results suggest that this N gradient (or some other variable that is correlated with N) further helps to explain the differences in plant quality that drive the Serengeti migration. In particular, the high N content of grasses in the plains may be the key factor driving the movement of the migratory grazers into this habitat at the onset of the rains. When the rainy season begins, green grass biomass rapidly increases throughout the ecosystem, but the higher quality

of the food supply in the plains compared with the woodlands may explain why the wildebeest leave the woodlands en masse at this time. As this supply dries up, green grass persists only in the woodlands, and the wildebeest are forced to move northward (McNaughton 1979*b*). The migration thus permits exploitation of an N-rich resource pulse that arises predictably each year.

The EP model of Boone et al. (2006) used a different approach to reach a broadly similar conclusion: the wildebeest migration is driven by a combination of rainfall and NDVI that together comprise an index of forage availability. We note that in the EP model, when two areas have equal NDVI, wildebeest do not choose areas with higher rainfall (and thus grass production) at any given time, but rather areas in which the ratio of current rainfall to total annual rainfall for a site is highest (Boone et al. 2006). In the wet season, this ratio is highest in the plains, so the wildebeest move there, but it is difficult to see in practice how assessing this ratio provides a plausible mechanism to explain movement onto the plains. The comparison between our model and that of Boone et al. (2006) indicated a better fit (27.4% vs. 13.4% of blocks with wildebeest present or observed in agreement) of our model at a 5-km resolution (fig. 6). This suggests that the incorporation of digestive constraints and plant protein content provide more reliable information about the resources that wildebeest seek than NDVI. We show here that incorporating additional factors such as plant N concentration helps account more fully for the seasonal movement into the plains, and the drive to exploit areas of high protein intake (when available) could provide a concrete mechanism to explain the migration. Given that Serengeti ungulates tend to enter a period of protein deficiency toward the end of the dry season (Sinclair 1977), it would
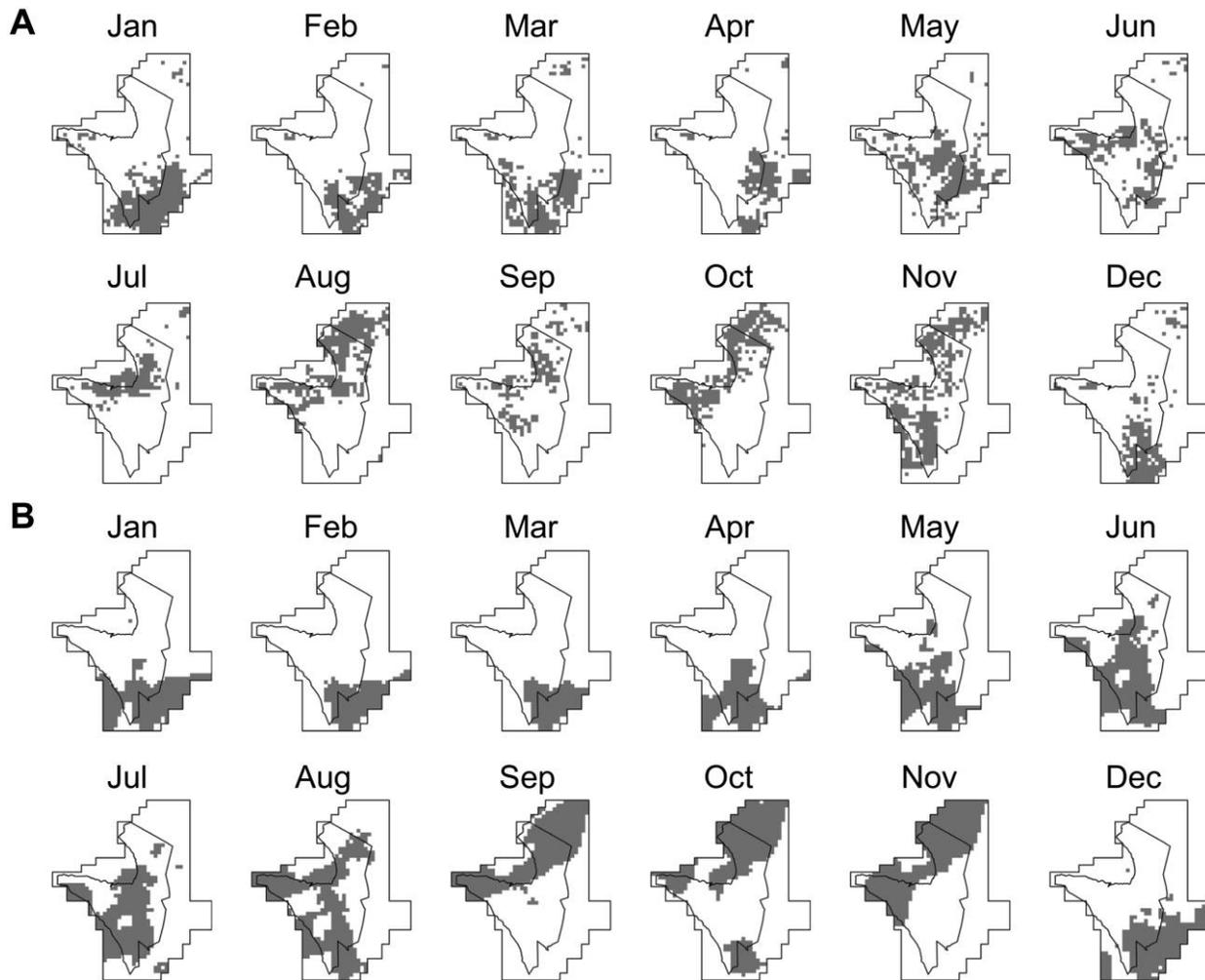
Figure 6: Monthly wildebeest distributions from the recce data (*A*) and predicted by the best-fit ordinary least squares model (*I,T,N*) at 5-km resolution (*B*), with filled cells representing mean values of ≥250 individuals calculated over the period August 1969–August 1972.

not be surprising if high-protein areas were rapidly sought out at the onset of the wet season.

Tree-Grass Competition, Water Availability, and Other Factors

Our conclusions regarding the potential importance of the suppressive effect of tree cover on grass biomass in determining wildebeest movement patterns are somewhat scale dependent. There is a negative correlation between tree and grass cover in savannas (Scholes and Archer 1997). All else being equal, the presence of trees in the woodlands and their absence in the plains should therefore result in a greater amount of grass biomass per unit area in the latter, and this difference could play a role in attracting wildebeest to the plains at times when grass is

available. Our results do show that including tree cover in the model increases the modeled migration distance (fig. 3*A*) compared with simpler grass biomass or intake models, so tree-grass competition does play some role in facilitating the migration. These results are less apparent at the broader spatial scale, although it is possible that heterogeneity in tree cover is more important in determining wildebeest distribution patterns at finer scales, and loss of information that results from aggregating data at the broader spatial scale masks these effects. An alternative possibility is that at a local scale, woody cover is correlated with risk factors (e.g., predation).

Conversely, the distribution of water supplies helps to explain wildebeest distribution patterns at the broader scale (25 km) but not at 10 km. The value of our water availability index (flow accumulation) varies widely over

fine spatial scales, depending on the idiosyncratic location of major rivers. Two very dry cells could differ greatly in terms of their proximity to water but would be treated identically in our model. This is more likely to lead to poor fits at the finer scale, since at the broader scale this heterogeneity becomes diluted. Regardless of these scale differences, however, the quantitative contribution of flow accumulation to model fit is minor. In the resource function Z we use in the model, food and water are combined additively (table 1). Our parameter estimates suggest far greater variation in the effect of the food term than in the water term (table 2), so the latter is likely to be influential only at the end of the dry season, when the food term tends to zero and water is scarce.

Past work has suggested than Na can play an important role in the behavioral ecology of Serengeti ungulates (McNaughton 1990; Tracy and McNaughton 1995; Wolanski and Gereta 2001). Ungulates often experience Na deficiencies, especially during pregnancy and lactation (Michell 1995), and select habitats and foods that offset these deficiencies (Belovsky and Jordan 1981; Holdo et al. 2002), so we hypothesized that the distribution of plant Na across the landscape might influence wildebeest migratory movements. In the end, this was not supported by our model. We note, however, that our model fit is poor during the transition period when wildebeest typically move into the western corridor (fig. 4), where soil and plant Na levels appear to be high (McNaughton 1988). It is also at this time that lactation demands are high and Na stress likely to be particularly important (Michell 1995). The lack of fit could thus be due to uncertainty in our plant Na GIS layer, leading to poor spatial agreement between the animal distribution and plant Na layers. Unlike N, which shows quite a consistent southeast to northwest gradient across the Serengeti, Na appears to show a more complex spatial pattern, with pockets of high Na within a low-Na matrix (fig. 2F). As a consequence, the unbalanced sampling on which the maps are based results in greater uncertainty in Na than N mapping (since most cell values in the lattice are based on interpolated quantities). Further sampling of soil and plant nutrients across the landscape may clarify this issue and shed light on the reasons for the preference of wildebeest for the western corridor at the beginning of the dry season.

Spatial Scale of Resource Tracking

A key finding of our model is that the size of the local neighborhood that wildebeest track and move within is as important as the overall spatial distribution of resources and seasonality in determining the migration. In our model, migratory behavior is an emergent property that arises from an adaptive movement framework when wil-

debeest are able to track resources in a neighborhood with a radius of at least 80 km and thus compare conditions at this scale with conditions in their current location for making movement choices. If their ability to track resources remains highly localized, the model predicts that they would not undertake the long-distance movements that are necessary to generate the migration.

That wildebeest can respond in real time to environmental cues to modify their migratory behavior has long been known. Early studies of the Serengeti migration showed that wildebeest and other species respond to both intra- and interannual fluctuations in the spatial distribution of resources, most likely forage or surface water linked to rainfall events (Swynnerton 1958; Grzimek and Grzimek 1960; Talbot and Talbot 1963; Pennycuick 1975; McNaughton 1979a). These researchers noted that migration routes and the timing of movement are highly variable from year to year (Swynnerton 1958; Talbot and Talbot 1963; Pennycuick 1975), prompting McNaughton (1979a, p. 57) to prefer the term "nomadic" rather than "migratory" to describe wildebeest movements. It must be pointed out, however, that factors other than large-scale perception may drive wildebeest to move out of local resource patches. We assumed in our model that the average wildebeest makes adaptive "decisions" based on immediate comparisons among sites, but our results could also fit models with behavioral components involving memory and genetically encoded movements.

We can outline several possibilities. At one extreme, only real-time environmental cues and/or social information drive the migration. It has long been noted that wildebeest appear able to track stochastic rainfall events (and thus flushes of green grass) over large distances (Talbot and Talbot 1963; McNaughton 1979b). Moreover, a combination of environmental and social cues picked up by animals in a widely dispersed herd could give rise to an "effective range" of perception that is greater than the local neighborhood of any given individual (Grunbaum 1998; Couzin et al. 2005; Couzin 2007). Couzin et al. (2005) and Grunbaum (1998) provided a theoretical framework for such an expanded effective range of perception, showing that when social information from even a few individuals is conveyed to the group, collective behavior emerges that effectively tracks resources across the landscape. By combining local environmental information and direct perception of long-distance cues with social cues from the larger herd, wildebeest may be able to move effectively up "noisy" resource gradients, leading to an emergent seasonal migration. For an isolated individual, this task may be impossible when conditions are variable (Couzin 2007). Although our model does not directly include social cues, it strongly suggests that extended per-

ception neighborhoods are a prerequisite for effective landscape-level exploitation of resources by wildebeest.

At the other extreme, the timing of and route taken during the migration are better understood as evolved traits resulting from selective pressure imposed by a long-term moving average in spatiotemporal patterns of resource availability (Boone et al. 2006). This seems unlikely to us, given the demonstrated correlation between time spent in wet and dry season ranges and rainfall abundance across years (Pennycuick 1975). A third hybrid possibility is that the migration is the result of simultaneous short-term responses to local environmental conditions coupled with navigation-driven movements (stemming from past experience or genetically coded behavior) acting at larger spatial scales (Bailey et al. 1996; Fritz et al. 2003; Mueller and Fagan 2008). The latter coarse-scale driver would permit wildebeest to explore areas beyond their local neighborhoods. This would have a synergistic effect on social information mechanisms and extend the effective perception range of the herd, allowing wildebeest to move up noisy environmental gradients with greater efficiency. Large-scale environmental trends, being more predictable than small-scale fluctuations, may become internalized over time by migrating herbivores, either through individual experience or as a selective force (Boone et al. 2006), and used as a tool for moving up noisy resource gradients. The poor fit of the wildebeest distribution to environmental factors during the transition period (May–July), when wildebeest move to the western corridor for the rut (Talbot and Talbot 1963), may be explained by a switch from environmental cues to a navigational mode during this period (Mueller and Fagan 2008). This switch could allow wildebeest to find the rutting site at the appropriate time. Memory (the past experience of an individual or herd) has been identified as an important mechanism in the movement behavior of large herbivores (Bailey et al. 1996; Dalziel et al. 2008) and may well play a role during this period and cause a deviation from the short-term resource-optimization strategy that operates at other times.

Further research is required to infer the extent to which individually detected environmental versus social cues, and opportunistic versus learned or genetically determined behavior (and the scales over which they operate), drive the movement decisions of individual animals (Alerstam et al. 2003). Specifically, the simultaneous collection of data relating to environmental factors, movement (as opposed to the resulting distributional patterns), and social context (behavior of members of the same or other species) would provide a basis for teasing apart the contribution of social cues after controlling for environment, for example; also, a study of navigational skills and cues would provide a basis for understanding the contribution of memory to migratory patterns in wildebeest. It would be of particular interest to understand the contribution of social cues and memory and genetic factors in driving fluid "nomadic" migrations such as that of the wildebeest versus other types of large-scale movement behavior (e.g., strict to-and-fro migration) more typical of migratory systems (Alerstam et al. 2003; Mueller and Fagan 2008).

Conclusions

The two key elements in our model that unequivocally give rise to a seasonal wildebeest migration are the countervailing rainfall and fertility gradients that cut across the Serengeti. Rainfall acts as a seasonal "switch" that controls the availability (and to some extent, the quality) of grass biomass: the length of the growing season is positively correlated with the amount of rainfall received across the ecosystem (McNaughton 1985; Boone et al. 2006), so the dry plains have forage available only for a few months of the year, but that forage is of high nutritional value when available. Such opposing rainfall and fertility gradients are a common feature of African savanna ecosystems (Bell 1982; Ruess and Seagle 1994) and may thus play a role in driving ungulate migrations elsewhere on the continent, such as the white-eared kob (*Kobus kob*) migration of the Sudan (Fryxell and Sinclair 1988) or the wildebeest migration of the Kalahari (Williamson et al. 1988). Given strong enough gradients over short enough distances to make seasonal migrations feasible, our model results suggest that the rainfall-fertility correlation provides the necessary conditions for a migration to emerge. The necessity of a minimum "resource tracking window" threshold is a key insight into our understanding of how complex emergent phenomena such as migrations have at least the potential to be explained by the application of simple rules within an adaptive movement framework. Our results do not refute the existence of genetically programmed factors as contributing factors driving the migration but rather suggest that they may not be strictly necessary to explain it.

Acknowledgments

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