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Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models

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Abstract. Large-herbivore migrations occur across gradients of food quality or food abundance that are generally determined by underlying geographic patterns in rainfall, elevation, or latitude, in turn causing variation in the degree of interspecific competition and the exposure to predators. However, the role of top-down effects of predation as opposed to the bottom-up effects of competition for resources in shaping migrations is not well understood. We studied 30 GPS radio-collared wildebeest and zebra migrating seasonally in the Serengeti-Mara ecosystem to ask how predation and food availability differentially affect the individual movement patterns of these co-migrating species. A hierarchical analysis of movement trajectories (directions and distances) in relation to grass biomass, high-quality food patches, and predation risk show that wildebeest tend to move in response to food quality, with little attention to predation risk. In contrast, individual zebra movements reflect a balance between the risk of predation and the access to high-quality food of sufficient biomass. Our analysis shows how two migratory species move in response to different attributes of the same landscape. Counterintuitively and in contrast to most other animal movement studies, we find that both species move farther each day when resources are locally abundant than when they are scarce. During the wet season when the quality of grazing is at its peak, both wildebeest and zebra move the greatest distances and do not settle in localized areas to graze for extended periods. We propose that this punctuated movement in high-quality patches is explained by density dependency, whereby large groups of competing individuals (up to 1.65 million grazers) rapidly deplete the localized grazing opportunities. These findings capture the roles of predation and competition in shaping animal migrations, which are often claimed but rarely measured.

Key words: *center of attraction and repulsion; correlated random walk; forage quality; GPS radio-collar data; homing; landscape of fear; MCMC simulation; predator-sensitive foraging; Serengeti-Mara ecosystem; wildebeest,* Connochaetes taurinus; *zebra,* Equus burchelli.

INTRODUCTION

The global decline of terrestrial mammal migrations has raised serious concerns about the persistence of this unique landscape-scale biological process (Harris et al. 2009). Because migrations rely on large contiguous habitats across regional environmental gradients, the collapse of migratory systems around the world is an indication that these remaining wild areas are succumbing to increased human pressure, particularly habitat loss and landscape fragmentation (Bolger et al. 2008).

By moving large distances, migrants are able to escape the limitations of local food supply, resulting in superabundant populations that have unusually large impacts on ecosystems (Fryxell et al. 1988; Hopcraft et al., *in press*). For example, the seasonal movement of 1.24 million wildebeest in the Serengeti (Conservation Information Monitoring Unit 2010) affects virtually every dynamic in the ecosystem, including fire frequency and tree–grass competition (Dublin et al. 1990, Holdo et al. 2009*a*), biodiversity of grasses and animals (Anderson et al. 2007*b*), food web structure (de Visser et al. 2011), and the socioeconomic status of local people (Sinclair and Arcese 1995*b*, Sinclair et al. 2008). The profound impacts that migrations have on ecosystems necessitates an improved understanding of how and why

animals move. Progress in this field requires discerning the key factors that influence the choice patterns of individual animals within a population (Alerstam 2006, Schick et al. 2008, Morales et al. 2010).

Animal migrations are typically determined by seasonal access to high-quality food patches, which generally occur across gradients of soil fertility, rainfall, elevation, or latitude (Fryxell and Sinclair 1988, Alerstam et al. 2003). However, individual animals must also balance access to essential resources (especially food), while at the same time minimizing the exposure to risk—especially from predation and anthropogenic threats (Fryxell et al. 2008). For instance, North American elk (*Cervus elaphus*) move across an elevation gradient that determines the seasonal quality and quantity of forage (Frair et al. 2005, Hebblewhite et al. 2008), but local movement decisions are influenced by proximity to risks such as predation from wolves, or disturbance from roads and clear-cut logging (Hebblewhite and Merrill 2007, 2009, Frair et al. 2008). Similarly, the movement of Thomson's gazelle (*Eudorcas thomsoni*) in the Serengeti is closely related to periodic greening of the energy-rich short-grass sward (Fryxell et al. 2004, 2005). Populations of saiga (*Saiga tartarica*) migrate large distances over the Central Asian steppe along a latitudinal gradient of productivity determined by seasonal precipitation and frost (Singh et al. 2010). Mongollian gazelle (*Procapra gutturosa*) also move in relation to latitudinal gradients of frost, but their movements tend be more variable than those of saiga, despite living in similar environments (Ito et al. 2006, Olson et al. 2010, Mueller et al. 2011). Wildebeest (*Connochaetes taurinus*) in the Serengeti migrate over an opposing rainfall and soil fertility gradient (Holdo et al. 2009*b*) where high soil fertility areas attract large herds during the wet season and high-rainfall areas are a refuge during the dry season (Pennycuick 1975, Maddock 1979, Boone et al. 2006). However, it is not well understood how individual animals weigh the costs and the benefits of moving in response to food and predation in such a way that leads to an annual migration.

Animal migrations represent the sum total of a sequential series of complex movements: at the finest scale, minute-by-minute choices sum to daily displacements, which in turn sum to monthly and seasonal trajectories. Therefore, the fine-scale movements of migrants are nested within the coarser scale movements and these aggregate to an annual migration (Börger et al. 2011). Because the resources that migrants track are in a constant state of flux (such as standing biomass), understanding the factors that explain daily movement provides evidence for the drivers of annual migrations. However, the role of predation in shaping mammal migrations has received relatively little attention, with the notable exception of elk in North America (Frair et al. 2005, Hebblewhite and Merrill 2007, 2009). Predation risk for large herbivores in savannas is correlated with vegetation and topography that allow predators to ambush their prey, leading to somewhat predictable patterns across the landscape (Hopcraft et al. 2005, 2010).

Until now, no studies have compared the movement patterns of two sympatric migratory species to ascertain if the same landscape variables, such as those related to food vs. predation, influence the movement of both species equally. This comparative approach is potentially powerful because not only does it allow us to investigate how different environmental conditions affect the same individuals as they migrate between distinct landscapes, but also it allows us to compare how these distinct landscapes affect individuals of different species (a natural paired factorial experiment). For instance, both wildebeest and plains zebra (*Equus burchelli*) have similar and associated migrations in the Serengeti-Mara ecosystem (Hopcraft et al., *in press*) and yet these species are taxonomically unrelated (i.e., bovids vs. equids), with quite different digestive physiologies (the annual migratory cycle and maps can be viewed in Appendix A). Ruminants, such as wildebeest, are more efficient at digesting moderate-quality plant material than are hindgut fermenters, such as zebra (Foose 1982, Demment and Soest 1985). Hindgut fermenters offset their lower digestive efficiency by processing greater quantities of forage faster, which enables species such as zebra to gain sufficient energy from low-quality grass (Bell 1970, Ben-Shahar and Coe 1992). The maximum abundance of wildebeest in the Serengeti seems to be regulated by the availability of dry-season forage rather than predation (Mduma et al. 1999), whereas evidence suggests the Serengeti zebra population might be limited by predation, especially on juvenile age classes, rather than by the overall food supply (Sinclair 1985, Grange et al. 2004). Therefore, it is possible that zebra might be choosing where and how to move during the migration based on factors related to predation, whereas wildebeest might make choices based on food availability. We conjecture that these two species might make choices as to how to move based on very different attributes of the same habitat.

The development of state-space models that link the basic components of animal movement (such as the turn angle and the displacement distance between consecutive time intervals) with potentially complex covariates have advanced our ability to understand individual choice patterns. For instance, these models have been used to understand animal movement as a function of the spatial environment that an animal is moving through, such as rainfall and vegetation quality (Morales et al. 2004, Patterson et al. 2008, McClintock et al. 2012), or the social context (e.g., group size) within which an individual is embedded (Haydon et al. 2008). Furthermore, these methods enable us to discern the external environmental variables that attract, repulse, or have negligible effect on the local movement decisions, and hence on trajectories of individual animals. The appli-
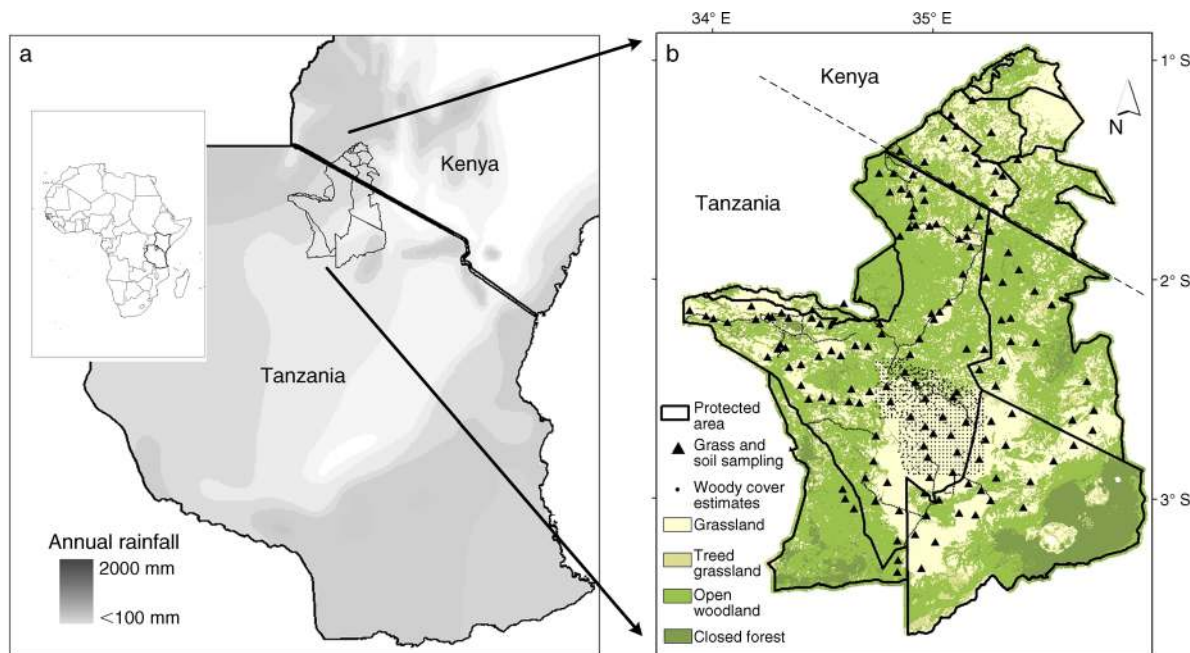
Fig. 1. (a) The greater Serengeti-Mara ecosystem lies between Kenya and Tanzania and coincides with a strong regional rainfall gradient. (b) Wildebeest and zebra move seasonally between open grassed plains in the southeast to woodland and open savanna areas in the west and north. Grass samples (triangles) and vegetation measurements (points along transects) were distributed across the rainfall gradient and in different habitat types.

cation of these more mechanistic "spatially informed" and "socially informed" methods to the study of migrations significantly advances predictive ecology, while their hierarchical nature facilitates fine-scale analysis of individual responses that captures many of the subtle individual differences in how animals weigh the costs and benefits of moving through a complex landscape.

The objective of this study is to determine how food quality, food abundance, and predation risk influence the distance and direction that migratory Serengeti herbivores choose to travel each day, and how these determinants differ between wildebeest and zebra. Because each tracked animal can be considered different to others, but not statistically independent, we used a hierarchical approach to model movement data from free-ranging wildebeest and zebra to determine which landscape variables best describe their movement. Hierarchical models account for the inherent variance between unique animals that is nested within the overall variance structure of the sampled population (Schick et al. 2008, Bestley et al. 2012). Based on the physiological differences between wildebeest and zebra and the factors regulating their overall abundance in the ecosystem, we hypothesize that (1) food quality affects the movement of individual wildebeest more than zebra, (2) the exposure to risk affects zebra movement more than wildebeest, and (3) food quantity affects both species most during the dry season, when resources are most

limiting. By contrasting the movement trajectories of these two sympatric species, we illustrate how research on individual choice patterns through hierarchical modeling expands our overall understanding of the drivers of animal migrations.

MATERIALS AND METHODS

The ecosystem and data

The movement trajectories of migratory wildebeest and zebra were studied in the Serengeti-Mara ecosystem, which lies on the border of Kenya and Tanzania in East Africa. The ecosystem extends from 1°30′ to 3°30′ S and 34°00′ and 35°45′ E, and is defined by the extent of the wildebeest migration (Fig. 1). Semiarid grasslands dominate the south, with mixed *Acacia* and *Commiphora* woodlands spread over the central and northern areas which are interspersed with large, treeless glades (Reed et al. 2008, Sinclair et al. 2008). The average annual rainfall increases from ~450 mm in the southeast to >1400 mm in the northwest (Fig. 1a), and falls primarily in the wet season (November to May). The ecosystem is described in detail by Sinclair et al. (2008).

We analyzed data from 17 female migratory wildebeest fitted with GPS radio collars between the years 2000 and 2008 (except 2002 during a transition period between funders) and 13 female zebra from 2005 to 2008 (see Appendix A for summary of collar statistics and Appendix B for details on animal capture, handling, and

GPS collars). In order to avoid the complications of fine-scale movement (Yackulic et al. 2011), we selected only the GPS locations at 18:00 hours (just before sunset when animals tend to congregate for the night; J. G. C. Hopcraft, *personal observation*), as we were interested in establishing the factors that influence the sequential movement between days that sum to the annual migration.

Models

The objective of this study is to understand how different environmental variables related to local food abundance, food quality, predation risk, and anthropogenic factors affect the daily movement decisions of zebra and wildebeest. Our approach is to estimate the parameters for a spatially informed correlated random walk, based on the approach introduced by Morales et al. (2004) to model elk movement. However, we extend this approach in two ways. Rather than modeling switches between discrete behavioral states (such as migratory vs. encamped), we model the parameters governing the distributions of daily steps (i.e., the displacement distance between consecutive daily locations) and turn angles (i.e., the absolute angle between straight lines linking three consecutive daily locations) as continuous logit or log-linked functions of environmental variables. We also adapted the approach to capture individual variation between collared animals by making the models hierarchical (see Supplement for the code and details in *Statistical analysis*).

We used a Weibull distribution to describe the daily step lengths. This is a nonnegative continuous distribution defined by a scale parameter α and a shape parameter β and has the following form:

$$W(x) = \alpha\beta x^{\beta-1}\exp(-\alpha x^{\beta}). \qquad (1)$$

The Weibull distribution is flexible, reducing to an exponential distribution when $\beta = 1$, having an exponential tail for $\beta \geq 1$ and a fat tail when $\beta < 1$. Furthermore, a Weibull distribution with shape parameter β equal to 2 is the theoretical expectation for displacements under a simple diffusion model, thus this distribution is well-suited for analyzing daily displacement distances (Morales et al. 2004). The mean displacement distance (d) as described by the Weibull distribution is given by:

$$d = \left(\frac{1}{\alpha}\right)^{1/\beta} \Gamma\left(1 + \beta^{-1}\right) \qquad (2)$$

where Γ is the Gamma function. Note that as the scale parameter (α) increases, the mean displacement decreases for a given value of beta.

We used the wrapped Cauchy distribution to model turning angles (Morales et al. 2004). The wrapped Cauchy is a circular distribution defined by the parameters ρ and μ and takes the following form:

$$C(\Phi) = \left(\frac{1}{2\pi}\right)\left(\frac{1 - \rho^2}{1 + \rho^2 - 2\rho\cos(\Phi - \mu)}\right) \qquad (3)$$

where $0 \leq \Phi \leq 2\pi$ and $0 \leq \rho \leq 1$.

The parameter μ describes the mean direction in radians. The parameter ρ describes the concentration around the mean such that as ρ approaches 1, the distribution becomes increasingly concentrated around the mean. When ρ approaches 0, the distribution is uniform in the circle, corresponding to an equal probability of movement in all directions.

The step lengths and turning angles of individual animals were linked to features of the landscape by modeling the scale parameter of the Weibull distribution α, and the variability and mean direction of turning angles (ρ and μ) as continuous functions of various landscape features that will be described in detail. Landscape features that cause animals to reduce their displacement distances (i.e., increase α) and increase the variability in turning angles (reduce ρ), resulting in an area-restricted search type of movement pattern, can be differentiated from the landscape features that cause animals to increase their daily step lengths (i.e., decrease α) and reduce turning angle variability (increase ρ toward 1), resulting in strong directional movement and a rapid exit from an area. We transformed turns to absolute values so that left-hand turns were equivalent to right-hand turns; therefore, μ could only range from 0 to π (0 implies directional persistence, whereas π indicates a complete turn in the opposite direction). Observation error was minimal at the scale of our analysis and therefore not included in the model: the average daily displacement was ~4 km, whereas GPS locations have approximately ±10 m error and locations were recorded at 18:00 hours local time every day ±3 minutes. Only data from sequential days were included in the analysis.

Landscape variables

GIS layers were constructed for eight predictor variables estimating food quality, food abundance, predation, and human disturbance at a spatial resolution of 1 km^2 (Table 1). The proximity of each animal's GPS locations to each of these landscape variables was calculated across all observations (except NDVI, normalized difference vegetation index). We tested for nonlinear relations by also including a quadratic function of the distance to each variable. The role of food quality was estimated from (1) the animal's proximity to high-nitrogen grass patches, (2) the 16-day mean NDVI value at the time and location of observation (i.e., the average greenness of the vegetation), and (3) the difference between the current 16-day mean NDVI and the previous 16-day mean NDVI values (positive values indicate greening, whereas negative values indicate drying). All of the NDVI layers were calculated from remote-sensing observations by NASA's MODIS satellite platform. Grass nitrogen was

TABLE 1. Explanatory variables included in the models predicting the parameters α, ρ, and μ for the Weibull and wrapped Cauchy models of animal displacement and turn angles.

Term	Definition
x_1	Standardized Euclidean distance of the ith individual at time t to patches of high grass nitrogen (patches in the upper 25th percentile of grass nitrogen).
x_2	Standardized 16-day mean NDVI value at the location of the ith individual at time t.
x_3	Standardized difference between the current 16-day mean NDVI value and the previous 16-day mean NDVI value at the location of the ith individual at time t.
x_4	Standardized Euclidean distance of the ith individual at time t to patches of high grass biomass (patches in the upper 25th percentile of grass biomass).
x_5	Standardized Euclidean distance of the ith individual at time t to patches of thick woody cover (patches in the upper 85th percentile of woody cover).
x_6	Standardized Euclidean distance of the ith individual at time t to drainage beds.
x_7	Standardized Euclidean distance of the ith individual at time t to pooled or flowing water (included in the analysis of movement in the woodlands, but not on the plains).
x_8	Standardized log of the Euclidean distance of the ith individual at time t to human settlements, weighted by population size of the settlement.

measured at 148 randomly selected sites across the Serengeti (Fig. 1) within all combinations of soil and vegetation types and across the rainfall gradient. Because the concentration of nitrogen in the grass is inversely correlated with the mean NDVI (see Appendix C), we regression kriged (Hengl et al. 2007, Bivand et al. 2008) the data from the 148 points with a 9-year mean NDVI layer (2000–2009) to generate an accurate estimate of the spatial distribution of grass nitrogen across the ecosystem (details provided in Appendix C). We estimated the Euclidean distance of the location of each animal at each time step to patches of high-nitrogen grass (defined as areas within the upper 25th percentile of grass nitrogen).

Grass biomass is positively correlated with soil moisture and rainfall, and negatively correlated with grass quality (Breman and De Wit 1983, McNaughton et al. 1985, Olff et al. 2002, Anderson et al. 2007a). Therefore we used the topographic wetting index combined with the long-term average rainfall over a 46-year period to estimate the biomass of grass available to the migrants (see Appendix C). Because animals might only require periodic access to areas with abundant grass biomass to supplement their diet (e.g., daily or seasonal foraging forays), the distance to high-biomass sites (defined as areas within the upper 25th percentile of grass biomass) was estimated for each animal at each time step.

Landscape features such as dense thickets or drainage beds conceal predators or provide predictable locations where predators might encounter prey (Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007, Kauffman et al. 2007, Valeix et al. 2009, Anderson et al. 2010). For instance, drainage beds are often associated with erosion embankments and confluences that help predators such as lions to catch prey (Hopcraft et al. 2005). Therefore, we used the distance to thick, woody cover and the distance to drainage beds to estimate the risk of predation. Most drainages in Serengeti are ephemeral freshets and do not necessarily contain water; access to surface water is determined separately. The

amount of woody cover available for stalking predators was measured systematically at 1-km intervals along 1882 km of transects over the entire ecosystem (Fig. 1) and the mean horizontal vegetative cover that could conceal a predator was assigned to each of the 27 physiognomic vegetation classes identified by Reed et al. (2008) and was mapped at a resolution of 1 km^2 (see Appendix C). We estimated the distance of each animal at every GPS location to the nearest thick cover (defined as cells above the 85th percentile of horizontal cover).

Access to water might be important for wildebeest and zebra and could influence their daily movement trajectories (Kgathi and Kalikawe 1993), so the distance to pooled or flowing water was estimated for all animals during the dry season only. During this time, water can only be found in the largest river systems (i.e., classes 1 and 2 of the RiversV3 layer in the Serengeti GIS Database; see Gereta and Wolanski 1998). During the wet season when migrants are on the plains, pools of rainwater are plentiful everywhere and access to drinking water is essentially unlimited, so we did not include proximity to water in the analysis of movement on the plains.

Exposure to human disturbance such as illegal hunting was estimated by measuring the proximity to human settlements and scaled by the density of people. Areas adjacent to high-density villages have large values and a high probability of illegal hunting (Hofer et al. 2000), whereas areas distant from low-density villages have small values (see Appendix C).

Statistical analysis

All landscape variables were standardized to zero mean and unit variance to facilitate cross-seasonal and cross-species comparisons. The parameters α, ρ, and μ of the Weibull and wrapped Cauchy distributions that are used to characterize movement were modeled as functions of landscape variables (Table 1) through log and logit links, respectively:

$$\log(\alpha_t^i) = b_0^i + \sum_{k=1}^{8} b_k^i x_{k,t}^i \qquad (4)$$

$$\text{logit}(\rho_t^i) = c_0^i + \sum_{k=1}^{8} c_k x_{k,t} \qquad (5)$$

$$\mu_t^i = \text{logit}\left(d_0^i + \sum_{k=1}^{8} d_k x_{k,t}\right)\pi \qquad (6)$$

where the subscript indicates the observation on day t for the ith individual (superscript) and there are eight environmental predictor variables (x_k) that are simultaneously measured on the same day t for animal i. The regression intercepts b_0, c_0, and d_0 are modeled hierarchically, with the superscripts "i" referring to the individual; therefore, each animal has its own intercept sampled from a population-level distribution. In addition, the regression coefficients b_k for α are also modeled hierarchically, allowing individual variation in step lengths between animals in response to each of the eight environmental variables. The individual-level coefficients are sampled from population-level distributions defined by hyper-parameters that are also estimated from the data. All population-level coefficients were modeled using normal distributions with uninformative priors for their mean and precision (1/variance). The shape parameter for the Weibull distribution (β) was modeled hierarchically but was not related to environmental covariates.

The models were fitted using WinBUGS (Lunn et al. 2000). We ran three chains with 100 000 iterations each, discarding the first 10 000 as burn-in, and retaining 10 000 values for each parameter after thinning the chains to avoid autocorrelation. Convergence of the Markov chains was assessed using Gelman and Rubin's diagnostic from the CODA package in R (Gelman and Rubin 1992).

For each coefficient, we report the posterior mean as well as the 80% credible intervals corresponding to the highest posterior density (HPD) intervals. We report the results for the full models that include all covariates; a backward elimination process and model selection based on the DIC indicated that the simplified models tended to have a poorer fit (Appendix D). We also report the number of individuals whose HPD intervals for the α's did not include zero as part of the hierarchical analysis to assess the consistency of the response across individuals.

A preliminary comparison of wildebeest and zebra movement by broad habitat zones suggests that the step lengths and turn angles are most different while animals are on the Southern Plains and most similar while animals migrate through the mixed woodlands of the Western Corridor, the Central Woodlands, and the Maasai Mara (Figs. 2 and 3). Therefore, the parameters describing mean daily step lengths (α and β) and the direction of movement (ρ and μ) were estimated for wildebeest and zebra on the Southern Plains separately from the mixed woodlands. Because we did not have complete annual GPS track logs for all animals due to damage and collar failures, the data set was subdivided (see Appendix A): of the 17 wildebeest collared, we had track logs for 15 of these individuals in the woodlands and 10 on the plains. All 13 zebra had track logs in both habitats.

RESULTS

The largest daily step lengths for wildebeest and zebra occur on the Southern Plains (Figs. 2 and 3); step lengths in the Western Corridor, the Central Woodlands, and the Maasai Mara are all shorter. Wildebeest have the greatest propensity to move forward rather than any other direction, with few 180° turns except on the Southern Plains; the largest steps (i.e., >12 km/d) generally occur up to 45° left or right of a straight line (Fig. 2). By comparison, zebra frequently return toward areas they occupied on previous days (i.e., turn angles of ~180°). Zebra make the largest step lengths (i.e., >12 km/d) when moving directly forward and sometimes backward, but rarely at 90° turns (Fig. 3). The shortest step lengths for zebra occur in the Maasai Mara, where zebra seldom move more than 2 km/d.

Results from the analyses of wildebeest and zebra movement (Tables 2 and 3, respectively) suggest that predation and food abundance affect the direction of turns (μ), the tortuosity of the movement (ρ), and daily distance moved (α) for wildebeest and zebra differently. Wildebeest tend to respond to food-related factors (grass nitrogen, NDVI, and, to a minor degree, grass biomass), especially on the plains, but they become more responsive to predation-related factors (such as woody cover and distance to drainages) in woodlands, although the responses are not strong (Table 2, Figs. 4 and 5). In contrast, zebra balance access to high-quality food with avoiding the risky areas associated with predators and humans when resources are abundant on the plains, but when resources decline and they are forced into the woodlands, zebra focus on accessing enough food in high-biomass grass patches. Predator related factors do not effect zebra movement in the woodlands as much as they do on the plains (Table 3, Figs. 4 and 5). The responses of individual zebra tend to vary more than those of wildebeest, which behave very similarly to each other (Table 4). For instance, the proximity to nitrogen is an important covariate in predicting the daily displacement of zebra at the population level (α in Table 3), but examination of the individual posteriors reveals a great deal of individual variation (Table 4). Table D2 in Appendix D summarizes the population-level variance.

Wildebeest and zebra respond similarly to three factors. (1) Both species tend to move a long way each day when they are close to (or within) high-nitrogen grass patches on the plains, but not in the woodlands,
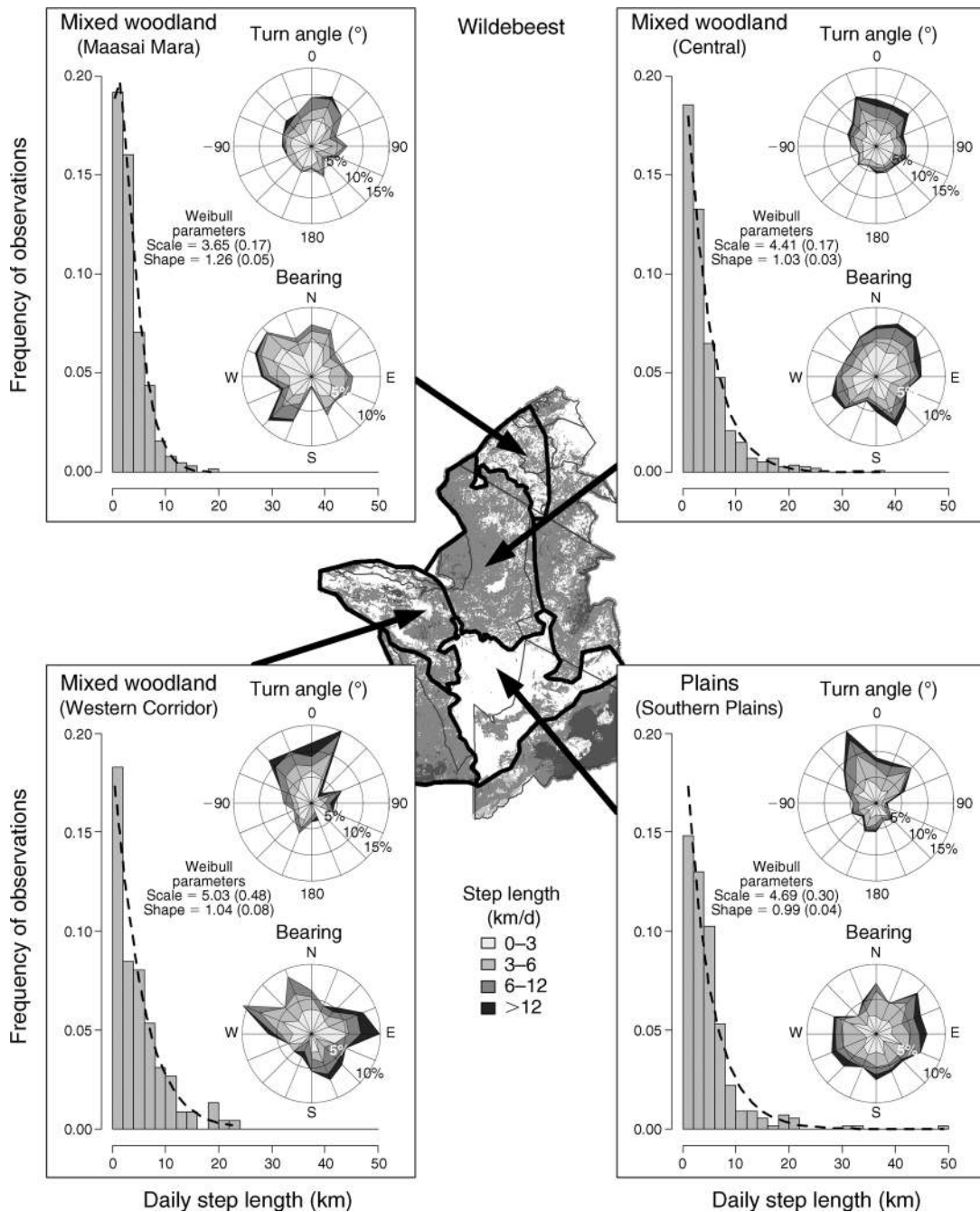
FIG. 2. Statistical properties of the daily movement trajectories of wildebeest change as they migrate. The longest daily step lengths occur on the plains, which are the wet-season range; the shortest steps occur in the northern dry-season refuge of the Maasai Mara. The largest steps (>12 km/d) generally occur between 45° to the left or right, and wildebeest rarely turn 180° around toward recently occupied patches (concentric circles represent 5%, 10%, and 15% of the observations). The dashed curved line overlaying the frequency histogram is the Weibull distribution, which is defined by the scale and shape parameters that describe the mean daily displacement distance and the spread of the distribution. A large scale parameter indicates large mean daily displacement distances, and large shape parameters indicate exponential tails; values in parentheses are standard deviations of the scale and shape parameters.

where their tendency is to move short distances each day (Tables 2 and 3, Fig. 4). (2) When NDVI is low (i.e., vegetation is dry), wildebeest and zebra move farther each day than when NDVI is high (i.e., vegetation is wet) in both the woodlands and on the plains (Tables 2 and 3, Fig. 4). (3) The response to humans is similar for wildebeest and zebra; both species move farther and change direction when they are close to high human densities than when they are far from humans; however, their movement tends to become less tortuous than
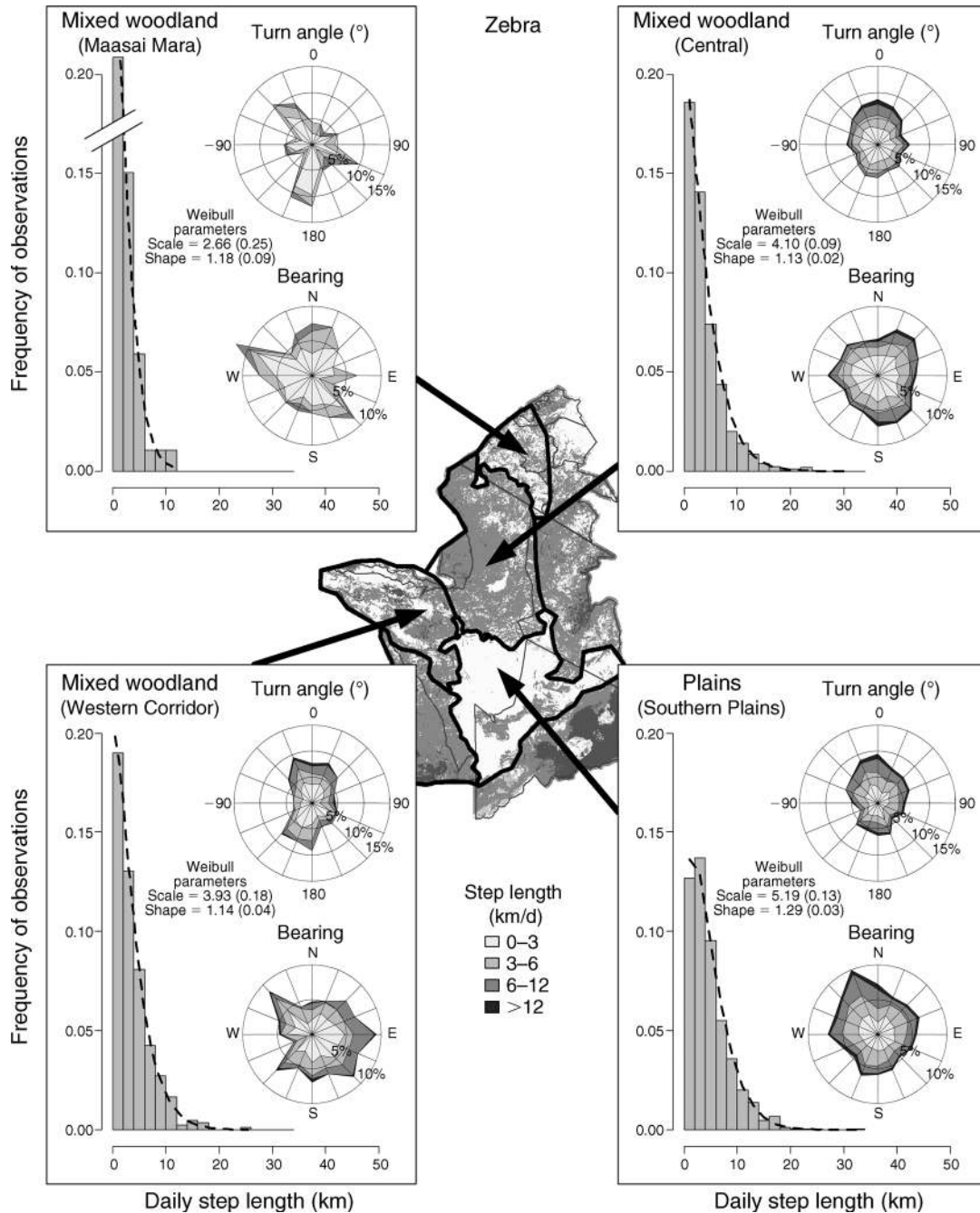
Fig. 3. Zebra tend to have the longest daily displacement on the Southern Plains and the shortest in the northern dry season refuge of the Maasai Mara. Zebra often return to previously occupied patches (i.e. turns of 180°) and generally make the largest steps (>12 km/d) when moving forward or returning (around 0° or 180°) and rarely to the left or right (90° or −90°).

usual when they are close to humans on the plains and more tortuous when they are close to humans in the woodlands (Tables 2 and 3, Figs. 4 and 5).

Wildebeest on the plains

Wildebeest on the plains move farther when they are close to high-nitrogen patches, or low-NDVI patches (dry vegetation), or near high-density human settlements. The daily displacement of wildebeest decreases nonlinearly (as described by the negative quadratic) the farther wildebeest are from high-nitrogen patches, with the largest daily displacement distances when they are in high-nitrogen grass patches (α in Table 2). All 10 individuals responded similarly to grass nitrogen (Table

4), which had the strongest effect on the distance wildebeest moved each day. Furthermore, while on the plains, wildebeest tend to change the direction of their movement in response to all of the variables except the proximity to drainages (μ in Table 2, Fig. 5). Grass nitrogen, proximity to humans, and the change in NDVI (greening processes) had the most pronounced effect on directional shifts (i.e., turn angles toward 0 and away from π; Fig. 5). Wildebeest movement tends to becomes more concentrated around the mean direction when animals are either near nitrogen-rich patches, near high-biomass grass patches, near humans, or far from woody cover (ρ in Table 2, Fig. 5).

Wildebeest in the woodlands

During the dry season when wildebeest recede into the woodlands, the distance that they move each day is determined by their proximity to high-nitrogen patches, the NDVI score, distance to water, woody cover, and human habitation. The distance wildebeest move between consecutive days in the woodland is negatively affected by their proximity to areas of high-nitrogen grass and water, such that they move short distances when they are near, but long distances when they are far from grass nitrogen. However, when NDVI is low (dry) or wildebeest are near (or inside) areas with thick woody cover, or adjacent to areas occupied by humans while in the woodlands, they tend to move farther each day (α in Table 2, Fig. 4). The most pronounced effects are due to nitrogen and NDVI, where 15 and 13 out of 15 individuals responded, respectively (Table 4). There were no factors that alter the turn angles of wildebeest in the woodlands except proximity to woody cover and drainages; however, the response was weak (μ in Table 4, Fig. 5). Similarly, proximity to woody cover was the only factor that caused wildebeest to move more directionally in the woodlands, but the response was weak (ρ in Table 4, Fig. 5). There appears to be much variation in the response of wildebeest in the woodlands to humans; although the 80th HPD percentiles included zero (Table 2), wildebeest tend to move directionally when they are far from humans (Fig. 5).

Zebra on the plains

Zebra move farther each day on the plains when they are close to high-nitrogen patches, when NDVI is low (i.e., the area is dry), or when they are close to humans (α in Table 3, Fig. 4) than when they are far. Conversely, zebra tend to move less each day when they are near woody cover or near drainages on the plains. The strongest effects are in response to NDVI, woody cover, and humans, which respectively caused 13, 7, and 10 out of 13 zebra to respond similarly (Table 4). All of the factors except distance to humans had an effect on the turn angle of zebra on the plains, but none were strong (μ in Table 3, Fig. 5). Only NDVI and humans affected the directionality of zebra movement; greening processes (i.e., a positive change in NDVI) caused zebra on the

plains to move more linearly than normal, and when zebra were far from humans, any anthropogenic effects became obsolete (ρ in Table 3, Fig. 5).

Zebra in the woodlands

The distance that zebra move each day while they are in the woodlands during the dry season is determined by their proximity to high-nitrogen patches, high-biomass grass patches, and water, which tend to decrease the distance that zebra move, whereas low NDVI scores (dry areas) increase the distance that zebra move each day (α in Table 3, Fig. 4). However, individual zebra showed a large amount of variation in how they responded to these factors; less than half of the total number of individuals ($n = 13$) had 80% of their posterior density beyond zero (Table 4), indicating inconsistent responses between animals. Zebra's proximity to dense woody cover and humans causes them to switch the direction of movement in the woodlands, as does their proximity to high-nitrogen grass and high-biomass grass, but only weakly (μ in Table 3, Fig. 5). Only the distance to grass biomass affects their directionality; when zebra are far from high-biomass patches, they tend to move in straight lines (ρ in Table 3, Fig. 5). Although zebra appear to make reverse turns when they are far from humans in the woodlands (Fig. 5), the 80th percentiles of the probability distribution of the coefficient included zero at the population level (ρ in Table 3), suggesting that there may be a large degree of variation in how individual animals respond to humans. In general, the distance to woody cover and drainages (i.e., the factors associated with greater predation risk) have very little effect on the movement trajectories of zebra in the woodlands.

Discussion

Linking individual behavior with population dynamics is essential for making ecology a more predictive science (Schmitz 2008, Morales et al. 2010). The study of movement trajectories of individual animals enables us to distinguish the specific landscape variables to which migratory animals are responding, when these variables may be important, and if different migratory species are reacting to the same environmental conditions (Patterson et al. 2008). Although the general pattern of the Serengeti wildebeest and zebra migrations have been known for a long time (Pearsall 1959, Grzimek and Grzimek 1960, Watson 1967, Pennycuick 1975), and more recent studies have identified the drivers of these migrations at the population level (Boone et al. 2006, Holdo et al. 2009b; Hopcraft et al., in press), the specific cues to which individual animals are responding, until now, had not been empirically identified. Understanding how animals respond to local environmental conditions provides clues about the drivers of these large-scale annual migrations and the role of these in population dynamics.

TABLE 2. Population-level posteriors (with 80th percentile highest posterior density intervals, HPD, in parentheses) of the coefficients for variables affecting the daily turning angles and step lengths of migrating wildebeest in the Serengeti.

Variable	Plains, wet season ($n = 10$; $\bar{\beta} = 1.56$ (1.34, 1.72))		Inverse displacement distance, α
	Turn angle		
	ρ	μ	
Food quality			
Nitrogen	**−0.50** (−0.91, −0.08)	**0.72** (0.28, 1.09)	**0.64** (0.30, 1.00)
(Nitrogen)^2	0.08 (−0.09, 0.25)	−0.15 (−0.27, 0.00)	**−0.20** (−0.38, −0.03)
NDVI	−0.20 (−0.42, 0.02)	**0.25** (0.04, 0.42)	0.23 (−0.12, 0.57)
NDVI change	0.07 (−0.15, 0.28)	**−0.45** (−0.64, −0.26)	0.09 (−0.11, 0.28)
Food abundance			
Grass biomass	**−0.40** (−0.71, −0.10)	**0.29** (0.03, 0.56)	0.09 (−0.29, 0.48)
(Grass biomass)^2	−0.05 (−0.29, 0.21)	−0.03 (−0.25, 0.19)	−0.01 (−0.19, 0.18)
Water			
Water	X	X	X
(Water)^2	X	X	X
Predation			
Woody cover	**0.59** (0.24, 0.93)	**−0.44** (−0.71, −0.18)	−0.19 (−0.47, 0.07)
(Woody cover)^2	−0.10 (−0.25, 0.05)	0.04 (−0.07, 0.15)	−0.11 (−0.34, 0.12)
Drainage	0.00 (−0.34, 0.37)	0.01 (−0.26, 0.33)	0.19 (−0.12, 0.52)
(Drainage)^2	−0.03 (−0.2, 0.14)	0.07 (−0.06, 0.21)	−0.11 (−0.41, 0.13)
Anthropogenic			
Human	**−0.79** (−1.14, −0.38)	**1.26** (0.85, 1.60)	**0.69** (0.19, 1.19)
(Human)^2	−0.09 (−0.29, 0.27)	−0.01 (−0.62, 0.52)	−0.17 (−0.57, 0.17)
Intercept	0.22 (−0.32, 0.74)	−0.55 (−1.02, 0.09)	**−1.71** (−2.27, −1.12)

Notes: The parameter ρ describes the concentration around the mean; as ρ approaches 1, the distribution becomes increasingly concentrated around the mean. When ρ approaches 0, the distribution is uniform in the circle, corresponding to an equal probability of movement in all directions. The parameter μ describes the mean direction in radians. Here, β is the Weibull's shape parameter and $\bar{\beta}$ is the mean shape parameter across all individuals. Note that α, the Weibull scale parameter, is inversely related to the mean displacement distance, d, of the Weibull distribution (see Eq. 2) so that negative values indicate a positive relationship between the variable and the distance that the animal moves. Boldface represents coefficients whose mean credible interval is nonzero (i.e., 80% of the HPD is above or below zero). NDVI is the normalized difference vegetation index. During the wet season, when migrants are on the plains, access to drinking water is essentially unlimited and was not measured (marked with X).

TABLE 3. Population-level posteriors (with 80th percentile HPD in parentheses) of the coefficients for variables affecting the daily turning angles and step lengths of migrating zebra in the Serengeti.

Variable	Plains, wet season ($n = 13$; $\bar{\beta} = 1.45$, (1.40, 1.50))		Inverse displacement distance, α
	Turn angle		
	ρ	μ	
Food quality			
Nitrogen	−0.11 (−0.25, 0.03)	**−0.20** (−0.35, −0.06)	**0.11** (0.00, 0.22)
(Nitrogen)^2	0.10 (0.00, 0.19)	**−0.18** (−0.26, −0.09)	−0.05 (−0.12, 0.02)
NDVI	−0.10 (−0.21, 0.00)	**0.15** (0.06, 0.23)	**0.22** (0.16, 0.29)
NDVI change	**0.10** (0.00, 0.21)	**−0.20** (−0.30, −0.11)	0.01 (−0.09, 0.10)
Food abundance			
Grass biomass	0.11 (−0.05, 0.26)	**−0.35** (−0.50, −0.20)	0.08 (−0.02, 0.17)
(Grass biomass)^2	−0.03 (−0.09, 0.03)	**0.12** (0.06, 0.17)	−0.02 (−0.06, 0.01)
Water			
Water	X	X	X
(Water)^2	X	X	X
Predation			
Woody cover	0.13 (−0.02, 0.27)	**0.18** (0.05, 0.32)	**−0.14** (−0.22, −0.04)
(Woody cover)^2	−0.09 (−0.17, 0.00)	**0.22** (0.12, 0.32)	0.07 (−0.01, 0.15)
Drainage	−0.16 (−0.33, 0.02)	**−0.31** (−0.49, −0.15)	**−0.11** (−0.20, −0.01)
(Drainage)^2	0.07 (−0.01, 0.15)	0.04 (−0.03, 0.12)	0.02 (−0.03, 0.06)
Anthropogenic			
Human	**−0.26** (−0.47, −0.05)	0.29 (−0.02, 0.54)	**0.42** (0.21, 0.60)
(Human)^2	**0.07** (0.02, 0.11)	−0.04 (−0.09, 0.02)	**−0.13** (−0.23, −0.01)
Intercept	−0.15 (−0.35, 0.09)	**−0.48** (−0.79, −0.18)	**−2.27** (−2.45, −2.09)

Note: Symbols and definitions are as in Table 2.

TABLE 2. Extended.

Woodlands, dry season ($n = 15$; $\bar{\beta} = 1.28$ (1.21, 1.33))		
Turn angle		Inverse displacement distance, α
ρ	μ	
−0.01 (−0.16, 0.15)	−0.13 (−0.27, 0.02)	**−0.30** (−0.41, −0.21)
0.05 (−0.06, 0.17)	−0.01 (−0.11, 0.09)	0.01 (−0.06, 0.08)
0.00 (−0.09, 0.09)	0.03 (−0.04, 0.11)	**0.22** (0.14, 0.30)
0.06 (−0.03, 0.15)	−0.03 (−0.12, 0.06)	**−0.13** (−0.24, −0.01)
0.09 (−0.11, 0.29)	−0.13 (−0.31, 0.05)	−0.03 (−0.20, 0.14)
−0.02 (−0.07, 0.04)	**0.06** (0.01, 0.10)	−0.03 (−0.11, 0.07)
0.00 (−0.11, 0.11)	0.01 (−0.09, 0.11)	**−0.10** (−0.20, −0.01)
−0.03 (−0.1, 0.05)	**0.09** (0.02, 0.16)	−0.03 (−0.08, 0.02)
−0.14 (−0.25, −0.02)	**0.13** (0.03, 0.23)	**0.11** (0.04, 0.20)
0.10 (0.03, 0.17)	−0.05 (−0.11, 0.01)	0.01 (−0.08, 0.09)
−0.07 (−0.19, 0.06)	**0.12** (0.01, 0.25)	0.05 (−0.03, 0.14)
0.02 (−0.03, 0.08)	0.02 (−0.02, 0.06)	0.01 (−0.03, 0.06)
0.09 (−0.15, 0.31)	−0.13 (−0.35, 0.13)	**0.23** (0.07, 0.40)
−0.03 (−0.07, 0.03)	0.00 (−0.07, 0.08)	−0.03 (−0.09, 0.04)
−0.15 (−0.32, 0.04)	**−0.80** (−0.96, −0.63)	**70.01** (50.83, 99.99)

Unique movement trajectories in migratory herbivores

The two most important findings from this research are that (1) wildebeest and zebra respond to different environmental cues within the same landscape when selecting their migratory routes, and (2) both migratory species tend to move farther when resource availabilities are at their highest, which is fundamentally different than the way that resident or dispersing animals move

TABLE 3. Extended.

| Woodlands, dry season ($n = 13$; $\bar{\beta} = 1.22$ (1.18, 1.25))		
Turn angle		Inverse displacement distance, α
ρ	μ	
−0.05 (−0.13, 0.02)	**−0.16** (−0.25, −0.06)	**−0.11** (−0.17, −0.03)
0.00 (−0.10, 0.07)	**0.22** (0.12, 0.31)	0.04 (−0.07, 0.13)
0.02 (−0.03, 0.09)	0.03 (−0.03, 0.10)	**0.09** (0.02, 0.15)
−0.05 (−0.11, 0.02)	0.01 (−0.04, 0.08)	0.02 (−0.02, 0.05)
0.23 (0.08, 0.37)	**−0.16** (−0.32, −0.01)	**−0.16** (−0.28, −0.03)
−0.07 (−0.12, −0.02)	−0.02 (−0.07, 0.03)	**0.12** (0.01, 0.21)
−0.05 (−0.15, 0.05)	−0.04 (−0.14, 0.06)	**−0.06** (−0.12, 0.00)
0.06 (0.03, 0.10)	0.00 (−0.03, 0.02)	−0.01 (−0.04, 0.03)
0.03 (−0.06, 0.14)	**0.34** (0.23, 0.45)	0.08 (−0.01, 0.17)
−0.03 (−0.08, 0.02)	**0.07** (0.00, 0.13)	0.02 (−0.04, 0.06)
−0.05 (−0.13, 0.04)	−0.07 (−0.14, 0.01)	−0.03 (−0.08, 0.01)
0.02 (−0.02, 0.07)	−0.02 (−0.04, 0.00)	0.00 (−0.03, 0.03)
0.09 (−0.23, 0.38)	**0.92** (0.48, 1.45)	0.03 (−0.10, 0.15)
−0.21 (−0.34, 0.01)	−0.41 (−0.72, 0.01)	0.00 (−0.01, 0.02)
−0.16 (−0.30, −0.03)	−0.25 (−0.53, 0.04)	**−1.83** (−1.94, −1.70)
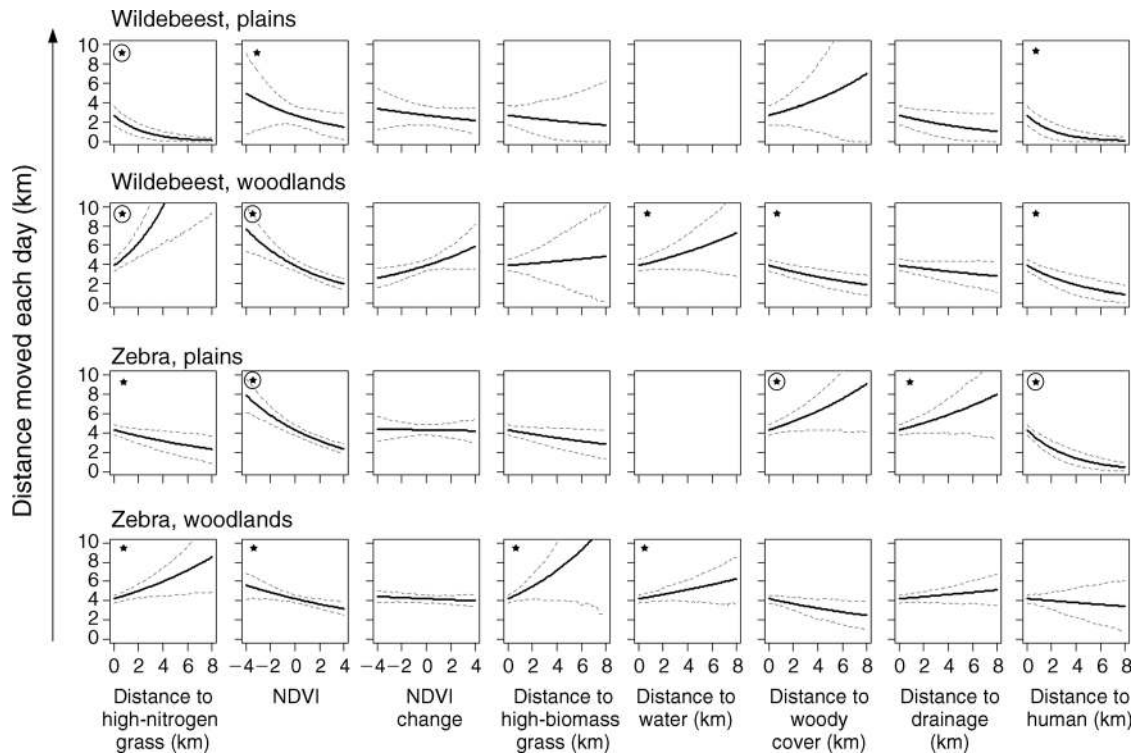
FIG. 4.   The distance moved each day by migratory wildebeest and zebra (i.e. daily displacement α) in response to landscape and environmental features. Both species move farther each day when close to high-nitrogen grass on the plains during the wet season when fresh grazing is most abundant, but move less when close to high-nitrogen patches in the woodlands during the dry season when fresh grazing is least abundant. The star symbol (★) corresponds to the boldface values in Tables 2 and 3, indicating that 80% or more of the HPD (highest posterior density) is beyond 0. The circled star corresponds to the boldface values in Table 4 and indicates that more than half of the individuals have 80% or more of the HPD beyond 0 (i.e., they react in a similar way).

(Morales et al. 2004, Hebblewhite et al. 2008). Although all migratory herbivores respond to large-scale gradients of climate (Harris et al. 2009), our results illustrate that the movement of individual wildebeest is almost entirely determined by access to high-quality grazing, with a weak response to predation in the woodlands. In contrast, zebra tend to balance predator aversion tactics with access to high-quality food, but compromise their safety during the dry season, when resources are most limiting, in favor of accessing high-biomass grass areas (Tables 2 and 3, Fig. 4).

The theory of animal movement predicts that individuals should maximize their time in high-quality sites and therefore move less and have a greater propensity for return movement when resource availability is high (witness the movement of elk in relation to their food supply; Morales et al. 2004, Hebblewhite et al. 2008). However, the results from wildebeest and zebra trajectories show the opposite response (Fig. 4); during the 4–5 month period of the year when grass quality on the Southern Plains is at its peak and large herds of wildebeest and zebra congregate in this area (Kreulen 1975, McNaughton 1985), these migratory species tend to move more each day than at any other point during the migration (Figs. 2 and 3). This result is counterin-

tuitive: why should animals move long distances every day when resources are at peak availability, rather than settling down and capitalizing on the good grazing?

Migratory animals tend to be more abundant than their resident conspecifics (Fryxell et al. 1988; Hopcraft et al., in press). The size of the migratory herds tends to change with season, and because all individuals in the group search for the same resources at the same time, the rate at which resources are depleted is proportional to the number of individuals in the herd. The results of the hierarchical modeling suggest that the daily movements of migratory wildebeest and zebra are consistently greatest when animals are in high-nitrogen patches on the plains. Furthermore, they respond to rapid greening processes by moving linearly and revert to tortuous movement as grasses dry (Tables 2–4, Figs. 4 and 5). These high-quality grazing areas attract up to 1.65 million other grazers at once (1.24 million wildebeest, 160 000 zebra, and 250 000 gazelle), which would deplete the grazing almost immediately and force animals to relocate on subsequent days in search of fresh grazing opportunities. The ephemeral nature of the high-quality grazing is heightened by localized thunder showers and the shallow volcanic soils on the plains, which result in rapid greening and drying cycles (de Wit 1978, Reed et
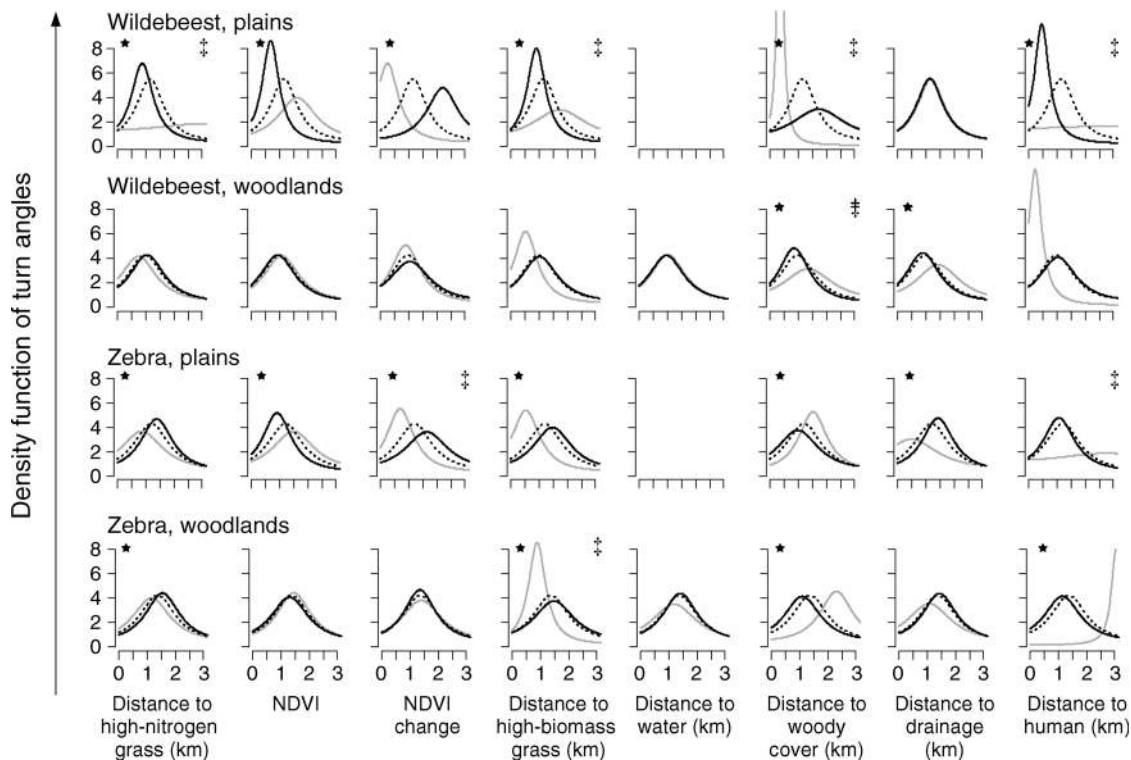
FIG. 5. The density function of turn angles from 0 to π for wildebeest and zebra as a function of landscape predictors. Dashed lines represent the animals' mean response, solid black lines represent the animals' response when the variable is at its minimum, and solid gray lines represent the animals' response when the variable is at its maximum. The star symbol (★) indicates that 80% or more of the HPD describing μ (direction of turn) is beyond 0. The double dagger symbol (‡) indicates that 80% or more of the HPD describing ρ (concentration of movement around the mean direction) is beyond 0. The star and double dagger symbols correspond, respectively, to the boldface values for μ and ρ in Tables 2 and 3.

al. 2008). The sudden and directed movement pattern by competing individuals, particularly lactating females, which require large amounts of high-energy forage (Hopcraft et al., *in press*), suggests that migrants might be forced to move farther each day during the wet season in order to find the best resource patches and to maximize their daily energy intake before the grazing is exhausted (Wilmshurst et al. 1999). This line of reasoning suggests that migratory animals living in very large herds (i.e., tens of thousands) might have very different movement trajectories than resident animals.

We propose that the tendency of individuals to move long distances when resource availability is at its highest arises as a result of density sensitivity. Therefore, the rapid and directional trajectories of potentially competing individuals searching for the best patches before the resource is completely depleted could be a feature of high-density migratory organisms (such as locusts (Buhl et al. 2006)) that differentiates them from roaming or seasonally dispersing organisms. Future research should focus on the resident subpopulations of wildebeest in the Serengeti, which we predict to have the opposite movement trajectories of migrants. That is, resident wildebeest should behave more like elk (Morales et al. 2004, Hebblewhite et al. 2008), with small steps in

nutrient-rich patches and large steps between patches because the small population of resident wildebeest (about 7000) would not deplete patches at the same rate as the large, migrant herds. This result would suggest that organisms living in high-density groups move differently than those in low-density groups, and that this is not a species-specific response.

There might be at least three alternative explanations for the long-distance movement of wildebeest and zebra when resources are at their peak. (1) Wildebeest and zebra could remain spatially unpredictable to predators by moving large distances when food is unlimited, while conserving energy when resources are scarce. However, the plains have very little cover to conceal predators and an individual's risk is most diluted in the wet-season mega-herds (Hopcraft et al. 2005, *in press*) so this is a less likely explanation. (2) Nonlocal factors such as day length or temperature might coincide with resource peaks, resulting in long-distance movement. However, large-scale factors such as day length and temperature do not vary greatly in equatorial regions (i.e., day length varies by 20 minutes between solstices and there is 10°C difference between seasons). (3) The scale of perception may vary across habitats such that animals on the open plains can see farther and move faster than when they

TABLE 4. The number of individuals in the hierarchical analysis of α where 80% or more of the posterior distribution describing the parameter is beyond zero, indicating how consistently individuals respond to each of the environmental covariates.

	Wildebeest		Zebra	
Variable	Plains ($n = 10$)	Woodlands ($n = 15$)	Plains ($n = 13$)	Woodlands ($n = 13$)
Food quality				
Nitrogen	**10**	**15**	**2**	**4**
(Nitrogen)^2	**4**	0	0	**2**
NDVI	2	**13**	**13**	**6**
NDVI change	0	**4**	2	0
Food abundance				
Grass biomass	1	1	1	**5**
(Grass biomass)^2	0	1	0	**0**
Water				
Water	X	**3**	X	**1**
(Water)^2	X	0	X	0
Predation				
Woody cover	0	**5**	**7**	3
(Woody cover)^2	0	1	2	0
Drainage	3	1	**2**	0
(Drainage)^2	1	0	0	0
Anthropogenic				
Human	**4**	**5**	**10**	0
(Human)^2	2	1	**4**	0
Intercept	**10**	**15**	**13**	**13**

Notes: Variables where the credible interval of the mean coefficient at the population level is nonzero are in boldface and correspond to the boldface values in Tables 2 and 3. Appendix D, Table D2 summarizes the population-level variance.

are in the closed woodlands. Models of the Serengeti migration suggest that wildebeest track conditions over an 80–100 km radius (Holdo et al. 2009b). Our empirical observations suggest that migrants match their movement trajectories with the spatial distribution of the resources, enabling them to exploit the seasonal availability of grazing most effectively. We argue that the fast and directed movement in areas where the grass is growing and senescing rapidly is further amplified by exceptionally large densities of grazers depleting the resource even more rapidly than expected.

Movement in the face of predation and starvation

The predator-sensitive foraging hypothesis (Sinclair and Arcese 1995a) proposes that as food becomes depleted, animals should take greater risks to obtain it. Therefore, the movement of wildebeest and zebra during the wet season should be different from their movement during the dry season, when food is most limiting. Results from the Markov chain Monte Carlo (MCMC) analyses of zebra movement generally conform to this prediction; however, wildebeest movement does not. The landscape features in which ambush predators are most successful at catching prey, such as woody cover and drainages (Hopcraft et al. 2005), caused most individual zebra to behave more cautiously by slowing their daily movements and changing their course of

direction only during the wet season, not the dry season. Wildebeest generally did not respond to landscape features related to predation on the plains during the wet season, and only weakly responded to them during the dry season (Tables 2–4, Figs. 4 and 5). Unpublished data from ground transects that repeatedly count wildebeest at different times of the year show that 91% of wildebeest observations are in groups of 10–3000 individuals (Appendix E), with 9% of observations in groups of 2–10 individuals. Wildebeest, unlike zebra, rarely occur alone and an individual's risk of being killed by a predator is diluted by living in exceptionally large herds, which might explain why very few individual wildebeest that we collared responded to the landscape features associated with predation, whereas zebra did (Tables 2 and 4, Figs. 4 and 5).

The Serengeti zebra population seems most likely to be regulated by predation on the juvenile age classes and by interspecific competition (Sinclair 1985, Grange et al. 2004), which suggests that zebra might be more sensitive than wildebeest to exposure to predators. During the dry season when good-quality grass is most limiting and starvation is most pronounced (Sinclair and Arcese 1995a), both wildebeest and zebra tend to move less overall (Figs. 2 and 3) and generally in response to food (Tables 2 and 3, Fig. 4). Most notably, the proximity to risky habitats weakly affects the direction in which zebra move, but no longer influences how far they move. Our results show that under dry-season conditions in the woodlands, individual zebra tend to move farther when they are in dry, low-quality habitats and might compensate by focusing on high-biomass grass patches in which they move short distances and less directionally than usual. Furthermore, during this dry period, they are less responsive than normal to risky habitats that could conceal ambush predators (Tables 3 and 4, Figs. 4 and 5), which supports the predictions of the predator-sensitive foraging hypothesis. An alternative explanation could be that zebra are no longer moving in response to predation in the woodlands because they are joining large herds of wildebeest and thereby gaining additional security (Sinclair 1985). This could enable zebra to access resources in risky areas that would otherwise be very dangerous, but may also expose them to greater grazing competition from wildebeest, in which case zebra could supplement their diet by consuming more grass biomass. Although we are unable to differentiate between these two explanations, data from ground transects illustrate that zebra are more likely to be associated with wildebeest in the woodlands than in the plains (Appendix F) and suggest that zebra may be choosing to migrate with wildebeest in riskier habitats.

Both wildebeest and zebra consistently move large distances each day and change the direction of their movement when they are close to areas with high human density (Figs. 4 and 5; Tables 2–4). This response emphasizes the fact that human disturbance can disrupt herbivore migrations even without causing direct mor-

tality, a threat that is often underrated in infrastructure development programs (Dobson et al. 2010).

When does a resource become a risk?

Grass biomass is an indicator of the abundance of forage available to herbivores; however, it is possible that tall grass also obscures prey sight lines and could conceal predators, similar to the effects of woody cover. Zebra in the woodlands consistently change their direction of movement and tend to move shorter distance each day when they are in patches with high-biomass grass (Tables 3 and 4, Fig. 4). One explanation for this slow movement is that zebra are selecting high-biomass patches because they are capable of extracting energy from relatively coarse forage due to their hindgut digestive physiology (Bell 1970, Foose 1982, van Soest 1996) and therefore can maintain a competitive advantage over ruminants, especially during the dry season, when resources are most limiting (Groom and Harris 2010). Alternatively, zebra might move less in these high-biomass grass patches because they are being cautious; their movement in these areas is very similar to their movement near drainages (Fig. 4), which are often associated with increased lion predation (Hopcroft et al. 2005). Whether the response of zebra to tall grass is due to the effects of predation as opposed to food abundance is not entirely clear, but it is probably the combined effect of both. In other words, zebra select high-biomass patches to supplement their intake rates, but in doing so, they increase their exposure to ambush predators. The point at which the resource becomes the risk for zebra is probably modulated by the availability of the resource, such that when resources are plentiful, animals can select any patch, but when resources are depleted, they are forced into a few patches and their presence becomes predictable for hunting predators. Therefore, the slow movement in high-biomass patches could be indicative of cautious movement by zebra or of depleted forage quality. In either situation, their reliance on potentially dangerous high-biomass patches may ultimately lead to a greater impact of predation on their populations than on wildebeest. Integrating data on the physiological condition of the animal in movement models (e.g., endocrine assays to distinguish hunger vs. fear) may clarify this ambiguity (Nathan et al. 2008).

Future research and the challenge of discerning memory

The role that memory has in determining the routes that migratory animals select is an interesting angle for future research (Morales et al. 2010, Smouse et al. 2010). Our analysis assumes that animals are responding only to the environmental conditions that they currently perceive in their immediate vicinity. However, presumably they have memory of previous conditions, which would be an evolutionarily advantageous trait for long-distance migrants (Milner-Gulland et al. 2011). Many of the variables that we measured affected the direction of turns (μ) and the concentration of turns around the mean direction (ρ) for both species (Tables 2 and 3, Fig. 5). The data show that collared wildebeest consistently move forward (with deviations up to 45° on either side), whereas zebra exhibit a greater propensity for return movement (i.e., turns of 180°) in all habitats and across all seasons (Figs. 2 and 3). Although it is tempting to say that wildebeest might be responding primarily to the current environmental conditions, whereas zebra might be combining their perception of the current situation with their memory of previous conditions (Brooks and Harris 2008), an equally likely explanation is that wildebeest do not return to previously grazed patches because they can remember that the resource has been depleted. Therefore, discerning the role of memory from the movement patterns alone remains very challenging and requires some additional knowledge about the state of the animal and condition of the previously used resource. Furthermore, there may be added costs associated with returning to recently grazed patches in terms of exposure to parasites dropped in the dung of previous grazers. Therefore, it might be evolutionarily advantageous to remember not to return too soon.

Conclusions

Our state-space modeling approach effectively identified specific environmental covariates that influence animal movement patterns at the population level and illustrates that: (1) different migratory species respond to different habitat dimensions, even in the same landscape; (2) the movement trajectories of grazers living in high-density herds is different from grazers at low density; and (3) animals seasonally trade off risk aversion tactics to access forage, and this influences their movement trajectories. Furthermore, the hierarchical aspects of the analysis enable us to capture individual variation in movement, which expands our understanding of the drivers of migration. Capturing the mechanisms by which individuals respond to environmental variability, such as large-scale shifts in rainfall patterns due to climate change, gives us greater power in predicting the migratory patterns of the population as a whole, and allows us to anticipate the ecological consequences that shifting migration patterns might have on nutrient cycles, disease transmission, or competition and predation interactions in the future.

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Supplemental Material

Appendix A

Overview of the annual Serengeti wildebeest migration including maps of the point locations of GPS collared wildebeest and zebra (by season) and a table summarizing the mean number of days tracked and distance moved per individual (*Ecological Archives* M084-012-A1).

Appendix B

Methods regarding animal capture and handling, animal morphometrics, and details of GPS collars (*Ecological Archives* M084-012-A2).

Appendix C

Additional material and methods describing how grass nitrogen, NDVI, grass biomass, the risk of predation, access to water, and exposure to anthropogenic risk were measured (*Ecological Archives* M084-012-A3).

Appendix D

A comparison between the full models presented in the manuscript and simplified models from a backward elimination process (*Ecological Archives* M084-012-A4).

Appendix E

Frequency histogram of the average wildebeest herd size estimated from systematic ground transects (*Ecological Archives* M084-012-A5).

Appendix F

Linear regression of the number of zebra observed as a function of the density of wildebeest by general habitat, suggesting that zebra might choose to stay near wildebeest in woodland areas where ambush predators are difficult to detect (*Ecological Archives* M084-012-A6).

Supplement

R and winBUGs code for running the hierarchical state-space models that link movement trajectories to environmental covariates (*Ecological Archives* M084-012-S1).