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Modelling the dynamics of migrations for large herbivore populations in the Amboseli National Park, Kenya

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ABSTRACT

The spread of human activity, settlement and land fragmentation threatens the migrations of large migratory ungulates in Africa. Modelling the migrations gives conservationists a tool for building scenarios of the threats and containment options. We propose a simple spatially explicit mathematical model of ungulate migrations based on the seasonal distribution of vegetation quantity and quality and allometric models of diet. We use the seasonal movements of selected migrants in relation to vegetation in the Amboseli ecosystem, Kenya. Parameters estimation was done by fitting the model to long term movement patterns by minimizing total least square errors. The model suggests that the migrants broadly track the shifting patterns of vegetation growth and senescence according to body size.

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1. Introduction

Africa's large mammal migrations face mounting threats, including human population growth, settlement, land fragmentation and habitat loss (Haris et al., 2009). Several models of seasonal migrations in ungulates have been proposed (Fryxell and Sinclair, 1988b; Fryxell et al., 2004; Mduma et al., 1999). Despite significant advances in the development of migration models (Taylor and Noris, 2007), they have found little application in conservation planning. The reasons range from models being too specific to species and context too complex for general application (Codling and Dumbrell, 2012). Most models also lack calibration and accuracy against known migrations (Haris et al., 2009). In our experience a lack of understanding and uptake of models by conservation managers is also a major impediment. Understanding the distribution and movement of animals in relation to resources is one of the great challenges in basic and applied ecology (Matsumura et al., 2010). Extensive research over the last few decades points to the seasonal shifts in the spatial distribution of pasture quality and biomass driving the seasonal migrations of large African ungulates (Vesey-Fitzgerald, 1965; Western, 1975; Bell, 1982; Fryxell et al., 2004). To overcome some of these limitations we have developed a model of ungulate migrations that is relatively simple and robust, can be calibrated against known migrations and used in ecosystem planning where there is a clear need for scenario building. The model is based on the seasonal shifts in the quality and abundance of vegetation and ungulate feeding selectivity derived from allometric models. We draw on four decades of ecological research and monitoring in the Amboseli ecosystem of southern Kenya (Western and Behrensmeyer, 2009) to test the model against the free-ranging pattern of movements prior to the disruption of migrations. We fit the model to long-term aerial data by minimizing total least square errors (Van Huffel and Vandewalle, 1991) thus allowing for seasonal variations. The model permits the investigation of the effect of body size on selection of pasture biomass and greenness and links species specific distributions and movement patters to pasture characteristics monitored on an ecosystem grid of 5 km by 5 km (Mose et al., 2012). The model can be applied directly to planning.

Body size has also been shown empirically to be a key factor governing the distribution of species in relation to pasture biomass (Western, 1973). Over the last three decades, a variety of allometric models have been developed to explain diet and feeding selectivity in ungulates (Illius and Gordon, 1992; Owen-Smith, 2002; Kshatriya, 1998; Demment and van Soest, 1985; Mduma et al., 1999). The models give a theoretical foundation for explaining the seasonal movements of ungulate species in relation to shifting pasture abundance and quality. Small bodied herbivores require more energy per unit of weight and have a more selective diet relative to large herbivores (Sensenig et al., 2010).

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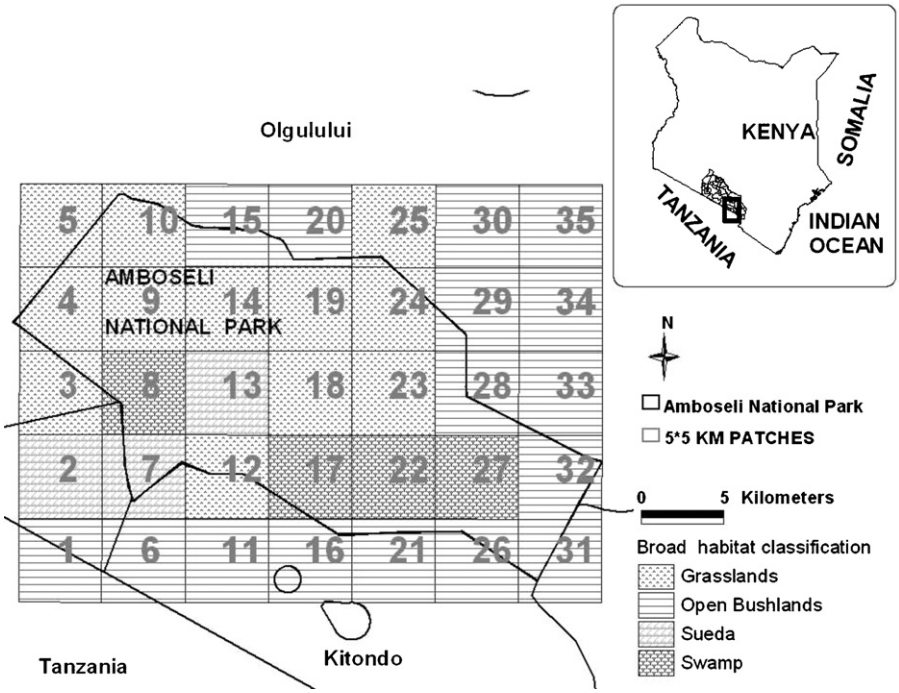

Fig. 1. Representation of the Amboseli basin area and the surrounding rangelands covering part of an 8300 km^2 ecosystem. The 5 km by 5 km grids are coded from number 1 to 35 and classified by habitat based on Western (2006).

In this paper we present a mathematical model of seasonal animal distributions for selected large wild mammal species (buffalo, elephant, wildebeest and zebra) in the Amboseli ecosystem. The spatially explicit model is based on vegetation quality and quantity. Percentage grass greenness is used as a surrogate measure of grass quality. The model also includes species habitat preferences and the effect of neighboring patches. The focus on the factors that broadly explain the migrations enables our model to be coupled to a population dynamics models developed by Mose et al. (2012).

The objectives of this paper are, first, to test how well a simple dispersal model based on vegetation quality, quantity and seasonal species aggregations fits the long term ecosystem monitoring data, second, to investigate the effects of body size on species distributions relative to pasture properties and, finally, provide a modelling tool for building scenarios of migratory movements.

2. Study area

The Amboseli ecosystem bestrides the Kenya-Tanzania border at the foot of Mount Kilimanjaro (Fig. 1). It lies at an altitude of 1200 m and receives an annual rainfall of 250–300 mm (Western and Behrensmeyer, 2009) with short rains generally falling in November and December and long rains from March to May (Altmann et al., 2002). The ecosystem includes Amboseli National Park and the surrounding rangelands. A system of swamps fed by the mountain forest catchment supports large populations of birds and mammals. Elephants and other ungulate populations migrate seasonally between the bushed grassland and the basin (Western, 1975). Historically, domestic and wild herbivores congregate in the swamps at the base of Kilimanjaro during the dry season and migrate to the neighboring bush lands and plains during the rains (Western, 1975). Rangeland fragmentation and the loss of key dry season grazing reserves have increased pressure on both livestock and wildlife. The gradual compression of herbivores into a smaller pasture area and the loss of flexibility due to sedentarization and land-use change (Worden, 2007), has led to a loss of large mammal production in the ecosystem.

3. Methodology

3.1. Sampling methodology of the long-term Amboseli data

The aerial surveys of large mammals and vegetation condition since 1974 cover an area of 8300 km^2 in eastern Kajiado, southern Kenya (Fig. 1). The counting methodology has been fully described by Western (1976). The sample design is based on systematic flight lines 5 km apart, overlaid on a 5 km grid system. The aircraft is flown at a nominal height of 91 m. Strips averaging 160–200 m wide are counted either side of the plane by observers. Population estimates and the standard errors of each species are calculated by treating each transect as a sample unit and using the Jolly method 2 (Jolly, 1969), as described by (Norton-Griffiths, 1978). In this paper long-term data was aggregated into two seasons (wet and dry). Spatial dependence (autocorrelation) between 5 km by 5 km patches is taken into account by the second term of the model which represents the effect of neighboring patches. We fit the model to wet and dry seasons distribution data separately.

Pasture conditions are assessed by the front seat environmental observer. Using both spectrometer measurement and cover estimates, green and total biomass is estimated (Western, 1976). Percentage greenness is further calibrated from small plots on the ground where dry and green fractions can be separated out (Western, 1976). For each of the 5 km by 5 km grids a value of grass biomass density and greenness is assigned and matched to corresponding large mammal population estimates calculated from Jolly method 2 (Jolly, 1969). In recent years, Normalized Difference Vegetation Index (NDVI) measurements of pasture have been used to validate the vegetation quality measures from aerial monitoring. NDVI therefore affords a fast and inexpensive method for estimating forage quality (Zhao et al., 2007). Preliminary analysis shows

no significant difference between percentage greenness estimates from the aerial surveys and those obtained by NDVI formulations.

3.2. Ecological factors in the model

We consider N patches corresponding to the 5 km by 5 km grids used in the aerial monitoring of large herbivores in the Amboseli area. The distribution model is spatially explicit and takes into account vegetation quantity represented by the density (kg/km^2) and vegetation quality (percentage of grass greenness). Grass greenness, being a proxy measure of grass quality, closely matches intake potential, digestibility and nutritive values of forage (Ball et al., 2001). Many studies have found a significant relationship between pasture greenness (especially chlorophyll concentration) and commonly used forage quality variables such as Natural Detergent Fiber (NDF), Acid Detergent Fiber (ADF) and Crude Protein Concentration (CP) (Ball et al., 2001).

Group-forming is a common behavior in many savanna ungulates (Pays et al., 2012), serving to monitor predators and increase information on pasture conditions. Large aggregating groups of ungulates in the African savannas heavily influence the movement and distribution of herbivores species (Fryxell, 1995). Furthermore species habitat preferences independent of food availability and quality could also play a role on their distribution. For instance, zebra and wildebeest may favor open bushland and grassland habitat to avoid predators even when the resource is not abundant (Thaker et al., 2010). We therefore refined our model by adding factors representing aggregation and habitat preferences by some species.

3.3. Mathematical formulation of the distribution model

We employ a model derived from Ideal Free Distribution (IFD) in which animals tend to spatially redistribute themselves proportional to resource availability (Kshatriya, 1998). Biomass quantity and quality in patch i are denoted by B_i and Q_i respectively. The number of animals that can be found in patch i is a function of a combination of B_i and Q_i. However in IFD, the number is proportional to B_i only. Furthermore the effect of forage availability and quality may not be linearly related to the species distributions and is likely to vary depending on a species grazing habits in relation to vegetation quality and quantity.

We assigned parameters α_j and β_j to quantity and quality of the food resource respectively. These parameters represent the respective importance of the two major factors determining the spatial distribution of species j. The higher the value of α_j the higher the influence of quantity in determining the distribution of species j. Values close to zero show a weak effect of quantity. The same applies for the parameter β_j associated with grass quality. In the model the number of animals of species j found in patch i is proportional to a combination of $B_i^{\alpha_j}$ and $Q_i^{\beta_j}$.

We assume that low numbers of species will be found in a given patch i if:

- Forage is abundant but is of low quality.
- Forage is of high quality but is scarce.

Sufficient and high quality grass is likely to attract many animals to a given patch leading to high densities in that patch. However intensive selection of high quality resource of low abundance may lead to its depletion forcing the species to increase selection of patches with abundant forage of low quality. The simplest combination that verifies the above assumptions is $B_i^{\alpha_j} Q_i^{\beta_j}$. We now refine the model, taking into account habitat preferences by adding a weight ρ_{ij} to patch i such that:

- $\rho_{ij} = 1$ if species j does not prefer the habitat type in patch i;
- $\rho_{ij} = \rho_j$ if species j prefers the habitat type in patch i.

The preferred habitats by the species were determined using Manley et al. (2002) method of habitat selection. The parameter ρ_j is also determined by minimizing the total least square errors between model estimates and observed data values. High values of ρ_j show a higher attraction of species j to its preferred habitats compared to other habitats. A value close to 1 implies an almost uniform attraction across all habitats. For the population of species j, the density on patch i is then proportional to $\rho_{ij} B_i^{\alpha_j} Q_i^{\beta_j}$. We also consider the potential to aggregate assuming that the population density of a given patch is influenced by the density in the neighboring patches. High densities of species in the neighboring patches tend to increase animal populations in a given patch. In Amboseli species seasonally congregate in the swamp habitat. We add a correction term in the model that corresponds to the expected population densities in the neighboring patches weighted by a parameter δ_j which is determined and represents aggregation ability of species j. A value close to zero indicates that the considered species does not show aggregation behavior. Finally the population of individuals of species j in patch i at a given season is proportional to:

$$G_{ij} = \rho_{ij} B_i^{\alpha_j} Q_i^{\beta_j} + \delta_j \sum_{n \in nb(i)} \rho_{nj} B_n^{\alpha_j} Q_n^{\beta_j} \tag{1}$$

where $nb(i)$ denotes the indexes of the neighbors of patch i, and the parameters α_j, β_j, δ_j, and ρ_j are associated with grass quantity, grass quality, the effect of neighboring patches and possible habitat preference by the migrants respectively. High values of G_{ij} show that species j favors patch i, thus leading to a higher proportion in patch i. The parameter values are obtained by minimizing the total least square errors between the model estimates and the data values. Different values may be obtained depending on whether wet or dry season. Let η_{ij} be the measured density of species j in patch i aggregated over a given season. We introduce $\overline{\eta}_{ij}$ the normalized density (density of species j in patch i divided by the total densities of species j in all the patches considered). Density $\overline{\eta}_{ij}$ is then the observed proportion of individuals of species j found on patch i. $\overline{G}_{ij}$ denotes the normalized density for population j on patch i given by the model. These transformations standardize the data without losing the relative contribution of each patch. The parameter values are obtained by minimizing the total least square errors presented by:

$$\Omega(\alpha_j, \beta_j, \delta_j, \rho_j) = \sum_{i=1}^{N} (\overline{G}_{ij} - \overline{\eta}_{ij})^2 \tag{2}$$

Then the model fit mean square error (MSE) for species j is:

$$MSE_j = \frac{1}{N-p} \sum_{i=1}^{N} (\overline{G}_{ij} - \overline{\eta}_{ij})^2 \tag{3}$$

where N is the total number of observations (patches) and p denotes the number of model parameters. The parameters obtained are associated with the minimum MSE shown in Tables 1 and 2.

4. Results

The model (1) was fitted to dry and wet season distribution data for different sized ungulates. The data were aggregated by the seasons determined and recorded during the sampling periods (Western, 1976).

Table 1
Dry season results. Average body weights w [kg], parameter values associated with minimum total least square error, mean square error and proportion of variance explained (R^2) by the model for each species.

Species	w [kg]	α	β	δ	ρ	Minimum mean square error (MSE)	R^2
Buffalo	450	0.7581	0.3387	0.3261	5.1613	13.02	0.664
Elephant	1875	0.4258	0.4195	0.0138	3.0645	8.61	0.556
Wildebeest	143	0.1523	0.7806	0.0133	2.0968	4.21	0.729
Zebra	200	0.2155	0.7710	<0.001	1.4516	2.79	0.723

Source: Amboseli Conservation Program (ACP).

Table 2
Wet season results. Average body weights w [kg], parameter values associated with minimum total least square error, mean square error and proportion of variance explained (R^2) by the model for each species.

Species	w [kg]	α	β	δ	ρ	Minimum mean square error (MSE)	R^2
Buffalo	450	0.3871	0.5806	0.0203	1.7742	21.39	0.475
Elephant	1875	0.3226	0.5484	<0.001	2.0968	12.31	0.439
Wildebeest	143	0.1935	0.1290	<0.001	1.4194	3.05	0.342
Zebra	200	0.2103	0.0010	<0.001	1.2903	1.72	0.214

Source: Amboseli Conservation Program (ACP).

4.1. Dry season distributions

The model fit for dry season showed that the species considered in the study moved in relation to food abundance and its quality. Parameters (α_j, β_j, δ_j, ρ_j) obtained as a result of minimizing the total least square error are summarized in Table 1. Values different from 0 for α, β and δ, and higher than 1 for ρ show significant effect of quantity, quality, aggregation and habitat preference on animal distributions, respectively.

Model results for buffalo, elephant, wildebeest and zebra explained close to 66%, 56%, 73% and 72% of the variance more than the respective mean models. Fig. 2 shows the model results and data values for zebra and wildebeest dry season distributions in each patch according to habitat type.

The figure illustrates how the model predictions of species distributions mimic the actual animal distributions in the Amboseli basin area.

For all species considered here, distributions were mainly driven by vegetation quantity and quality ($\alpha, \beta > 0$). Large animals notably buffalo and elephant were more influenced by quantity ($\alpha > 0.42$) than by quality ($\beta < 0.42$). For relatively small bodied species, the effect of quality was very high ($\beta \approx 0.80$), while that of quantity, despite being significant, was much lower ($\alpha < 0.22$).

Buffalo showed strong aggregation aspect. According to the model results neighboring patches contributed almost 33% of the combined effects of vegetation quality and quantity on species distribution.

The aggregation effect was very low for zebra. The large body sized animals favored some particular habitats (higher values of ρ).

4.2. Wet season distributions

During the wet season, animals distributions seemed to be driven by vegetation quality and habitat preference. Aggregation effects were much lower and were not significant for elephants, wildebeests and zebra (Table 2). In particular, vegetation quality had very little influence on zebra distribution during this period. The model fits for each species explained between 21% and 48% more than their mean models. The large bodied animals significantly redistributed in response to a combined effect of vegetation quality and abundance (α and $\beta > 0.3$). Parameter values associated with quantity (α) were low for wildebeests and zebra (<0.22), as both species were spread out more randomly. Pasture is constantly renewed during wet season, rendering animals movements less sensitive to food flux. Compared to the dry season, large species showed less habitat preferences. Fig. 3 shows wet season model and data results for zebra and wildebeest.

5. Discussion

We have presented a simple spatially explicit mathematical model of migrations based on vegetation quantity and quality (grass greenness). The conservation of large migratory mammals depends on detailed knowledge of seasonal movements and variability in ranging patterns. This calls for long term monitoring data, which is lacking for most conservation areas (Reichman et al., 2011). We drew on the unusually long-running monitoring data for Amboseli to test our model. The model suggests that migrants in Amboseli broadly track the seasonal and shifting patterns of greening vegetation across the ecosystem in the dry period. The model accounts for more than 70% of the total variation in movements. Wildebeest redistributed themselves in response to a combined effect of grass abundance, quality, habitat and neighboring patch effects. The model also accounted for over 70% of the zebra movements but herds were more spread out ($\delta < 0.001$) and less susceptible to neighboring patch effects. The difference between species is explained by the non-ruminant tolerating a wider range of grasses than wildebeest (Owen-Smith, 2002). The random spread of zebra is also evidenced by the lowest minimum mean square error values (Tables 1 and 2) compared to other species. Wildebeest usually seek young high quality grass more easily digested by ruminants (Hanley, 1982). Thomson's gazelle, a smaller ruminant than wildebeest, is yet more selective (Fryxell et al., 2004).

Seasonal rainfall patterns govern the quantity and quality of vegetation and influence the large scale movements of herbivores. Our results show that wildebeest movements track these changes and account for 72.9% of the variation during the dry season. However, only 34.2% of the total variation was explained by the model during the wet period, possibly because of the extensive availability of vegetation exceeding minimum feeding requirements and the large choice of locations opened up by widespread availability of water (Western, 1975; Williamson et al., 1988). This is evidenced by the wet season model fits which show little species aggregation ($\delta < 0.001$). Furthermore individuals can move suboptimally either through error in patch assessment or for reasons other than resource abundance (Cressmann and Krivan, 2006) and its quality.

Forage quality and quantity are often inversely related (Van Beest et al., 2010), forcing large-bodied herbivores like elephant and buffalo to trade-off whether to select forage quantity at the expense

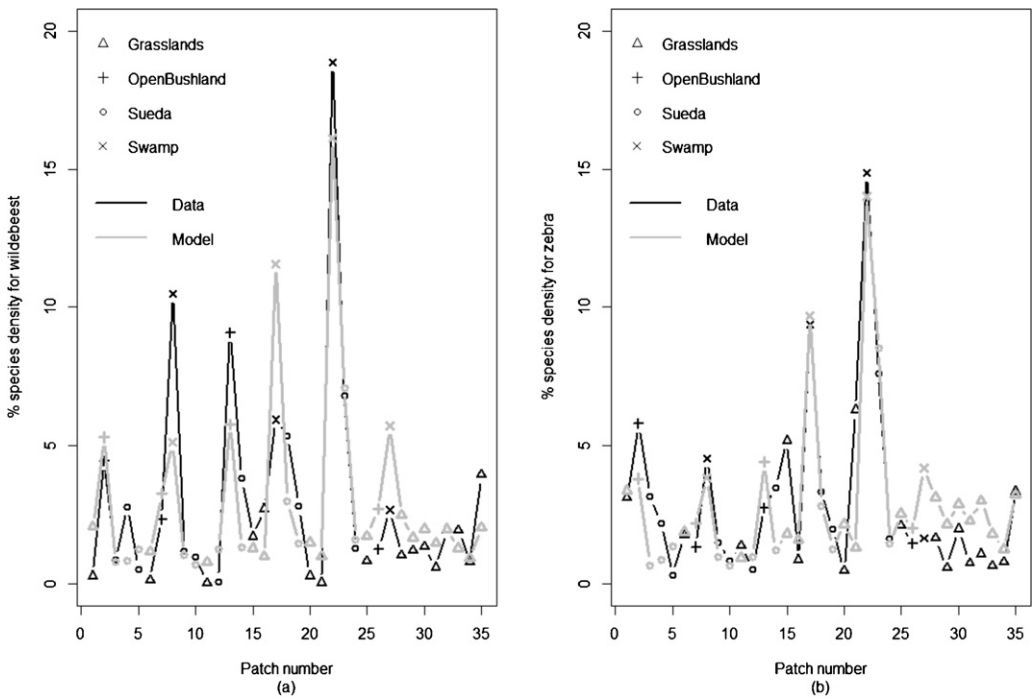

Fig. 2. *Dry season results.* Model output (in gray) showing percentage density distribution of wildebeest (a) and zebra (b) in each patch numbered 1–35 compared with actual distribution data (in black) for the Amboseli area. The habitat types in each patch are also shown.

of forage quality, especially during the dry period. According to our model, large species redistribute themselves in the patches in response to both quality and quantity. More evidence of trade-offs between food quality and quantity have been shown (Fritz and de Garine Wichatitsky, 1996; Bergman et al., 2001). The amount of variance explained by the model fit for elephant was 55.6% during the dry period. The fit dropped to 43.9% in wet seasons. Elephant movements were almost equally affected by vegetation abundance and quality (ratio of α to $\beta \approx 1$ during the dry season) but shifted to vegetation quality in wet seasons when pasture was abundant (ratio of α to $\beta = 0.59$) for a fixed percentage distribution in both vegetation quality and quantity. In general, vegetation quantity significantly affected the distribution of large-bodied species across seasons compared to quality, reflecting a higher daily

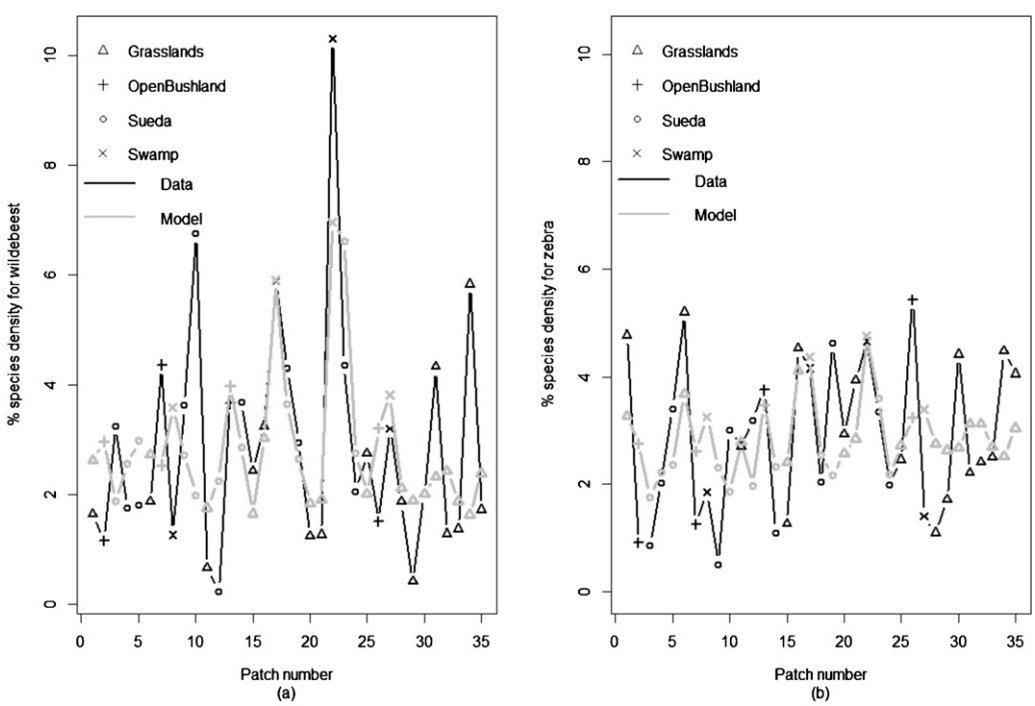

Fig. 3. *Wet season results.* Model output (in gray) showing percentage density distribution of wildebeest (a) and zebra (b) in each patch numbered 1–35 and actual distribution data (in black) for the Amboseli area. The habitat types in each patch are also shown.

food intake to meet metabolic requirements (Kshatriya, 1998). In Amboseli elephants and buffaloes congregate heavily on the high biomass swamp vegetation in the centre of the park during the dry season.

We found that zebra, wildebeest and elephant showed no significant neighboring patch effect ($\delta < 0.001$) in our model during the wet period. The model results show that animals distributed according to pasture quality and availability in the patches, as opposed to the vegetation conditions in neighboring patches. Buffalo were most affected by aggregation effect. The model suggests they concentrate on high density green patches of forage. One explanation is that buffalo graze down one patch because it is green and abundant and that there is no large advantage in moving to an adjacent patch with similar vegetation conditions.

Since forage is constantly renewed during the wet season and higher quality outside the Amboseli basin, grazing species move to the surrounding pastoral lands. The few resident wildebeest redistribute themselves in response to a combination of greenness and quantity. Wildebeest movements are more influenced by the grass greenness than grass abundance measured by height (Wilmshurst et al., 1999). Similar results are presented by our model especially during the dry period as seen in Table 1. Here wildebeest distribution tracked vegetation quality ($\beta = 0.7806$) and quantity ($\alpha = 0.1523$).

While parameter estimates obtained from the model did not show a clear pattern when plotted against species weight, this is likely due to the small number of species included in our model. A comprehensive study of all herbivore species in Amboseli is required to establish the relationship between body size, pasture conditions and species feeding selectivity.

6. Conclusion

To be useful to conservation planning and management, large herbivore migration models must mimic actual movement patterns. We have presented a spatially explicit mathematical model that does closely reflect movement patterns established from long-term monitoring studies in the Amboseli ecosystem. We show that the migrants track the seasonal shifting patterns of vegetation quality and quantity consistent with the Ideal Free Distribution model of animal forage (Kshatriya, 1998) and with allometric diet theories (Illius and Gordon, 1992) of the differential movements between species. The results show that a relatively simple and generalized mathematical model of seasonal herbivore migrations can be developed for use in conservation planning and management. Our model can most usefully be applied in generating scenarios of the impact of changing land uses and climate on grassland ecosystems. The model can utilize high resolution satellite data such as Normalized Difference Vegetation Index (NDVI) to guide in identifying species migration corridors and dispersal areas other than the relatively expensive aerial surveys. Furthermore, such analysis can be used to validate the model. Most of Kenya's wildlife is found outside protected parks and are facing increased competition for space from rising human population, agricultural expansion and other pressures such as drought and possible climate change. The amount of variance explained by our model and the graphical comparisons with actual wildlife distribution censuses, show that the model can provide a solid foundation for mapping of species utilization zones for conservation purposes. It also forms a strong basis for incorporating more variables, such as seasonal rainfall, terrain, temperatures, water distribution and so on, into the model and using Bayesian techniques to determine the influence of human behavior on wildlife migrations.

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