

# 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

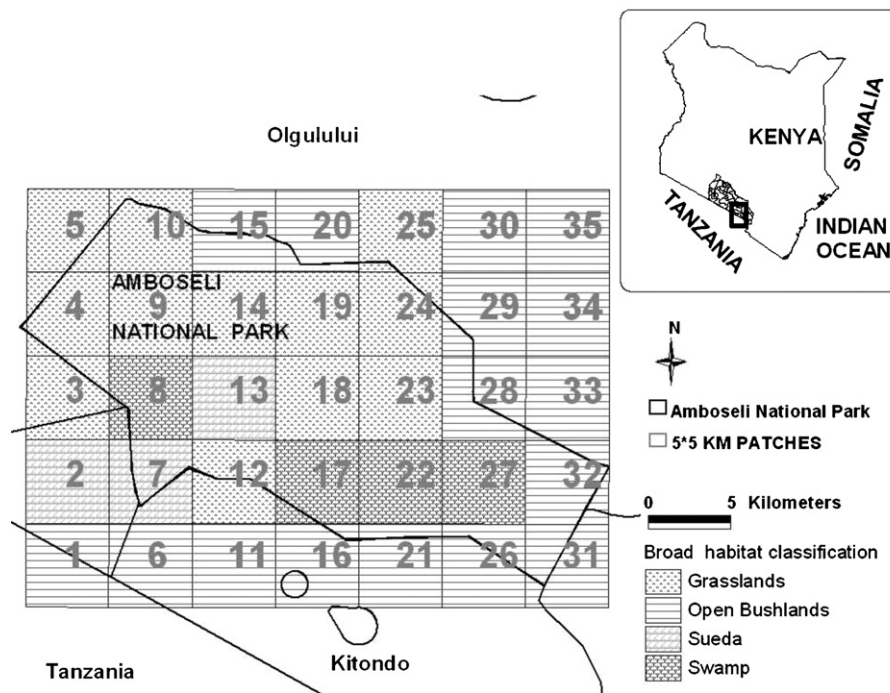
Africa's large mammal migrations face mounting threats, including human population growth, settlement, land fragmentation and habitat loss (Haris et al., 2009). Several models of seasonal migrations in ungulates have been proposed (Fryxell and Sinclair, 1988b; Fryxell et al., 2004; Mduma et al., 1999). 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 Huffer 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 patterns 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<sup>2</sup> 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 Behrensmeier, 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 bushy 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<sup>2</sup> 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

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