

## LETTER

## Landscape scale, heterogeneity, and the viability of Serengeti grazers

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### Abstract

Species persistence can be threatened by substantial temporal variation in food resources over time. On the other hand, spatial heterogeneity in resources at the landscape scale might allow mobile consumers to compensate for temporal variability in resource availability at the local scale. We evaluated this hypothesis, using an extensive data set on foraging, grass growth, and movement by Thomson's gazelles living on the Serengeti Plains. Here we show that modelled populations of Thomson's gazelles can only persist under Serengeti conditions in the face of observed levels of rainfall stochasticity by making adaptive movements to take advantage of ephemeral spatial distributions of food resources. More importantly, our models suggest that Thomson's gazelles in Serengeti require unrestricted access to relatively large areas of grassland (> 1600 km<sup>2</sup>) to guarantee long-term persistence, particularly when there is positive spatial autocorrelation in resource abundance, as is the case in Serengeti. If this proves to be true for other species and/or other systems, then understanding of complex behavioural responses to spatially and temporally heterogeneous food supplies may be essential to successful conservation of grazing herbivores.

### Keywords

Extinction, grassland, herbivore, lattice, model, movement, population viability analysis, Serengeti, Thomson's gazelles.

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### INTRODUCTION

Food resources of many wildlife species often vary considerably over time (Mduma *et al.* 1999; Post *et al.* 1999; Bjørnstad & Grenfell 2001). Temporal variability in resource abundance can threaten long-term persistence of consumers, provided that periods of low resource abundance are common enough and severe enough to drive consumer populations to levels at which chance demographic events or Allee effects come into play (Boyce 1992; Morris & Doak 2002). On the other hand, resources also vary spatially across all ecological landscapes. By adaptively selecting profitable resource patches at the landscape scale,

we hypothesize that mobile consumers may be able to compensate for unfavourable temporal variation in resources experienced at smaller spatial scales. Although population movement across complex ecological landscapes has been the focus of much recent work (Kareiva & Odell 1987; De Roos *et al.* 1991; Hassell *et al.* 1991; Neubert *et al.* 1995; Lima & Zollner 1996; Ranta *et al.* 1997; Lambin *et al.* 1998; Blasius *et al.* 1999; Grenfell *et al.* 2001), spatially-explicit landscape models have rarely been used to consider long-term population viability (Morris & Doak 2002).

We recently showed that the shifting mosaic of Thomson's gazelles (*Gazella thomsoni thomsoni* Günter) on the Serengeti Plains can be predicted by adaptive foraging

models (Fryxell *et al.* 2004), based on experimentally derived parameters relating to foraging success and grassland productivity and nutritional quality (McNaughton 1985; Wilmshurst *et al.* 1999). Here we use this information to develop simulation models, to test the implications of landscape scale and resource heterogeneity on the long-term persistence of Thomson's gazelles.

## METHODS

All of our simulation models include dynamic interactions between Thomson's gazelles and grassland plants, with temporal and spatial patterns of gazelle abundance shaped by both demographic and behavioural responses to plant abundance. Serengeti grasslands support a mix of graminoids and forbs, both of which are fed upon by Thomson's gazelles and most other large herbivores. For simplicity, however, we will refer to plants on the Serengeti plains as if they were all grasses.

We assume a stochastic, seasonal environment, with a dry season alternating with a wet season of stochastically variable length. State variables in the model are updated at daily time steps. Wilmshurst *et al.* (1999) sampled the spatial distribution of Thomson's gazelles on the Serengeti Plains every two weeks along transects of 220 km in length. These transects overlaid a set of rudimentary vehicle tracks criss-crossing a 40 × 40 km portion of the Serengeti Plains, with the NW corner of the study area located at 2°32.1' S, 34°57' E. After lumping the gazelle spatially-explicit census data into 10 × 10 km cells, 16 of which comprised the study area, Fryxell *et al.* (2004) used information theoretic methods to identify the most parsimonious movement model to explain patterns of gazelle redistribution from census period to census period. In order to apply the adaptive movement subroutine, the simulations described in this paper were accordingly conducted on a lattice representing the Serengeti Plains, with each lattice cell measuring 10 km × 10 km. Virtually all of the other parameters used in the model are also based on empirical observations in Serengeti.

Patterns of plant growth are based on McNaughton's (1985) measurements on the Serengeti plains showing a sigmoid relationship between number of days of growth and annual rainfall. We approximate this relationship by the following function:

$$\text{Growdays (rain per day)} = 65 + \frac{300e^{0.01 \text{ rain per year}}}{e^{0.01 \text{ rain per year}} + e^{6.25}}, \quad (1)$$

where rain per year is equal to annual rainfall. We assume average annual rainfall of 671 mm in the northernmost row and 529 mm in the southernmost row of our lattice, based on data from rain gauge stations 1 and 7 in Table 1 of McNaughton (1985) with average annual rainfall for

intermediate rows of the lattice interpolated between these values. Annual rainfall is assumed to be stochastic, but normally distributed, with a coefficient of variation of 25% of the local mean, based on the rainfall data summarized in McNaughton (1985). We assume that rain is distributed uniformly throughout the growing season, at a daily rate  $R = \text{rain per year}/\text{growdays}$  (rain per year). In some simulations, we assume that annual rainfall within each grid cell of the lattice is independent of that in other cells, whereas in other trials we repeat our simulations with positive spatial autocorrelation (with  $\rho$  ranging between 0.4 and 0.80) between neighbouring cells. In the latter case, the annual rainfall deviate in any given cell ( $\hat{z}_i$ ) is calculated using the random normal deviates drawn for that cell ( $z_i$ ) and any neighbouring cell ( $z_{i-1}$ ), modified by the autocorrelation coefficient ( $\rho$ ):  $\hat{z}_i = \rho z_{i-1} + [(1 - \rho^2) z_i]^{1/2}$ .

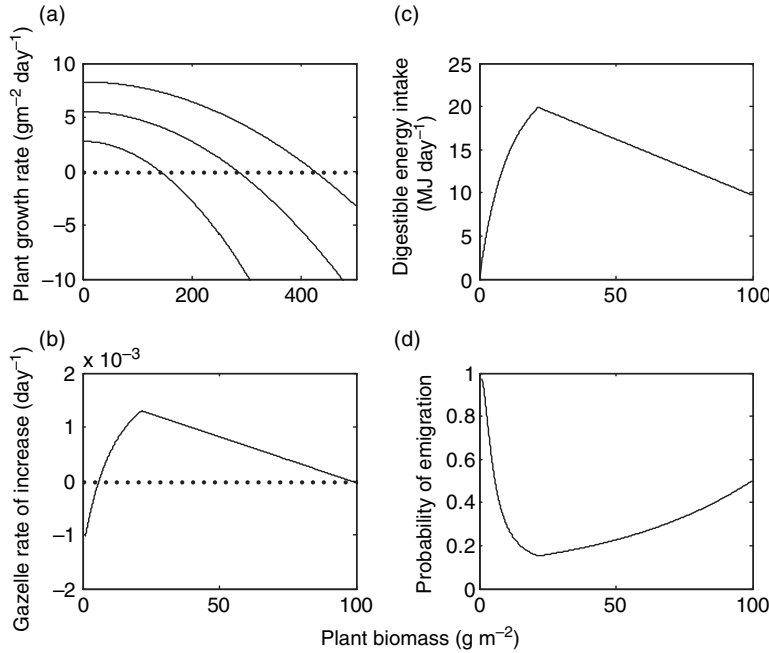
McNaughton (1985) measured biomass change over the first 30 days following the initiation of rainfall within permanent grazing exclosures. These measurements indicate that maximum daily grass growth (measured in g dry matter  $\text{m}^{-2}$  per day) is a positive function of daily rainfall  $R$  (measured in mm):

$$\omega(R) = -1.79 + 2.11R. \quad (2)$$

The maximum grass biomass in McNaughton's (1985) permanent grazing exclosures was  $\approx 280$  g dry matter  $\text{m}^{-2}$  in the most arid parts of the Serengeti Plains during a period in which daily rainfall averaged 3.462 mm. We accordingly link grass carrying capacity  $K$  to rainfall through the coefficient  $\Psi = 280/3.462 = 80.872$ . In the stochastic simulations,  $K(R) = \Psi R$ .

Fully parameterized models of grass growth in relation to moisture and standing biomass are scarce in the ecological literature. One of the most detailed attempts to model plant growth was Robertson's (1987) measurements on savanna grasslands in Australia, conducted as part of a decade-long collaborative study of the population dynamics of kangaroos and domesticated livestock in relation to rainfall (Caughley *et al.* 1987). This work showed that plant growth was related curvilinearly to plant biomass, with peak growth rates at low biomass. The peak of grass growth was scaled to rainfall. The pattern of growth in the Australia study was well represented by a nested series of quadratic curves. Similar logic has been used to model grassland dynamics in the face of grazing by voles (Turchin & Batzli 2001).

We accordingly represent the growth of Serengeti grasses by a modified logistic growth curve. Following Robertson's (1987) lead, we assume that the daily rate of grass growth during the wet season is at a maximum at low values of vegetation biomass ( $V$ ), declining curvilinearly with grass biomass according to the following function:



**Figure 1** Model relationships between grass biomass and (a) the daily rate of grass growth for a range of daily rainfall rates (bottom curve = 1.75, middle curve = 3.5, and top curve = 5.25 mm rainfall day<sup>-1</sup>); (b) the daily rate of population increase by Thomson’s gazelles; (c) the daily rate of energy gain by Thomson’s gazelles; and (d) the probability of emigration from a given patch. The probability of emigration was calculated on the assumption that average biomass elsewhere in the ecosystem was 100 g m<sup>-2</sup>. A different curve of similar shape would apply for any different level of grass biomass averaged across the lattice.

$$\frac{dV}{dt} = r_{\max}[V + K(R)] \left[ 1 - \frac{V + K(R)}{2K(R)} \right]. \quad (3)$$

For the growth rates observed in Serengeti,  $r_{\max} = 0.039 \text{ day}^{-1}$ , based on McNaughton’s (1985) data. The two in the denominator forces the maximum of the quadratic growth curve to occur at low grass biomass. This formulation yields a nested series of growth curves, whose maximum and equilibrium values are proportionate to daily rainfall  $R$  (Fig. 1a). In years with low rainfall, both the maximum rate of grass growth and the carrying capacity are markedly lower than in years of high rainfall. During the dry season, we assume that grasses decline at a daily rate of at least  $-1.79 \text{ g dry matter m}^{-2}$ , based on the intercept of the linear function  $\omega(R)$ , augmented additionally by consumption by any herbivores present.

At the end of the dry season, the standing crop of grass is reset to 0 and re-growth occurs from below-ground reserves. At this stage, we cannot say definitively how long such subsized (i.e. donor-controlled) re-growth can occur, but there is some evidence from re-clipping experiments in Serengeti that some grass species can cope with repeated episodes of above-ground defoliation (Braun 1973; J.F. Wilmshurst unpublished data).

Rates of consumption and energy intake by Thomson’s gazelles are based on Wilmshurst *et al.*’s (1999) experimental data. The hourly rate of energy intake is estimated by multiplying the hourly rate of consumption [ $X(V) = aV/(b + V)$ ] by a linear function describing the digestible energy content of forage [ $Q(V) = c - dV$ ], where  $a$  (the maximum hourly rate of consumption) = 380 g dry

matter h<sup>-1</sup>,  $b$  (vegetation biomass at which the rate of consumption is 1/2 the maximum) = 15 g dry matter m<sup>-2</sup>,  $c$  (maximum forage quality) = 0.011201 MJ g<sup>-1</sup> dry matter of grass eaten,  $d$  (the rate at which quality declines with increasing plant biomass) = 0.05 MJ m<sup>2</sup> g<sup>-2</sup> dry matter, and  $V$  is the plant biomass (in g dry matter m<sup>-2</sup>). All of these parameters were estimated from Wilmshurst *et al.*’s (1999) experimental trials using captive Thomson’s gazelles, spanning plant biomasses between 0 and 200 g dry matter m<sup>-2</sup>. This yields the following function for hourly energy intake:

$$Y(V) = \frac{aV(c - dV)}{b + V} \quad (4)$$

The daily rate of energy intake cannot be estimated by simply multiplying  $Y(V)$  by the daily foraging time, because most grasses decline considerably in nutritional quality as they grow and mature, replacing readily digestible components with indigestible lignin and poorly digestible hemicellulose (van Soest 1982). These changes mean that *ad libitum* consumption levels may fall below the level predicted by the short-term functional response considerations. Modelling this effect requires a second, digestive constraint, *ad libitum* consumption as a function of plant biomass [ $I(V)$ ]. Field measurements in Serengeti (Wilmshurst *et al.* 1999) indicated that digestible energy content of the sward declined with sward biomass in an approximately linear fashion. We accordingly use Wilmshurst *et al.*’s (1999) parameter values to model the digestive constraint (in MJ day<sup>-1</sup>) by the function  $I(V) = e - fV$ , where  $e$  (the maximum daily intake of energy) = 22.7 MJ day<sup>-1</sup> and  $f$  (the rate at which daily intake declines with sward biomass) = 0.13 MJ m<sup>2</sup> g<sup>-1</sup> day.

Daily energy gain (Fig. 1c), measured in MJ day<sup>-1</sup>, is calculated by taking the lesser of the constraint functions  $I(V)$  or  $Y(V)t_{\max}$  where  $t_{\max}$  (the maximum number of hours spent foraging each day) = 9 h day<sup>-1</sup>:

$$Z(V) = \min \left\{ \frac{aVt_{\max}(c - dV)}{b + V}, e - fV \right\}. \quad (5)$$

The daily rate of food intake, measured in g dry matter m<sup>-2</sup>, can be calculated similarly as the minimum of the following constraints, obtained by factoring out food quality:

$$W(V) = \min \left\{ \frac{aVt_{\max}}{b + V}, \frac{e - fV}{c - dV} \right\}. \quad (6)$$

Demographic parameters for Thomson's gazelles are not available, so we estimated these from allometric comparisons for African artiodactyls (Western 1979). The artiodactyl regression data suggest that the maximum per capita rate of growth equals

$$\Gamma(m) = 0.0000274 \times 10^{(3.18 - 0.35 \log_{10} m)} \quad (7)$$

where  $m$  is the body mass measured in g. For a 20 000 g Thomson's gazelle,  $\Gamma = 0.0013$  day<sup>-1</sup>. We further assume that the maximum rate of decline when energy intake is nil is similar in magnitude to the maximum rate of increase. In keeping with most consumer-resource models, the maximum rate of population growth is assumed to occur when energy intake is highest. Energy intake is accordingly translated into the per capita daily rate of population growth by the function  $dN/Ndt = \Lambda Z(V) - \Gamma$ , where  $N$  is population density of gazelles (individuals m<sup>-2</sup>),  $Z(V)$  is the daily rate of energy intake (MJ day<sup>-1</sup>),  $\Lambda = 0.00013$  is the rate of conversion of daily energy intake into daily gazelle population growth, and  $\Gamma$  is the maximum per capita rate of gazelle increase (or decline) per day (Fig. 1b).

Gazelles are assumed to redistribute themselves among neighbouring cells on the lattice, emigrating with probability  $\theta(V)$ . The underlying logic of this lattice model shares many features with several earlier models (Turner *et al.* 1993; Focardi *et al.* 1996; Farnsworth & Beecham 1999; Abrams 2000). The daily rates of change in gazelle population density  $N$  (modelled as individuals m<sup>-2</sup>) and plant biomass  $V$  (modelled as g dry matter per m<sup>2</sup>) averaged over each 100 km<sup>2</sup> cell  $ij$  (referring to row  $i$  and column  $j$  of the lattice) are accordingly calculated by the following system of equations:

$$\frac{dV_{ij}}{dt} = r_{\max ij} [V_{ij} + K_{ij}(R_{ij})] \left[ 1 - \frac{V_{ij} + K_{ij}(R_{ij})}{2K_{ij}(R_{ij})} \right] - N_{ij} [\Omega(V_{ij}) - \theta(V_{ij})] W(V_{ij}) \quad (8)$$

$$\frac{dN_{ij}}{dt} = N_{ij} [\Omega(V_{ij}) - \theta(V_{ij})] [\Lambda(V_{ij})Z(V_{ij}) - \Gamma] \quad (9)$$

where  $\theta(V_{ij})$  represents the probability of emigration from the focal cell and  $\Omega(V_{ij})$  represents the summed rate of immigration from neighbouring cells into the focal cell. Local redistribution rules and consequent patterns of cell-specific immigration vary among models: local energy-matching (most of the simulations) vs. simple diffusion (one set of simulations for comparative purposes). Local energy-matching has been shown to be much more consistent with the Serengeti field data than simple diffusion (Fryxell *et al.* 2004). For modelling purposes, gazelle density and plant biomass had to be in the same spatial units. Since we think that few readers would associate much practical meaning to gazelle density measured in individuals m<sup>-2</sup>, we quote gazelle densities in individuals km<sup>-2</sup> throughout the text and figures.

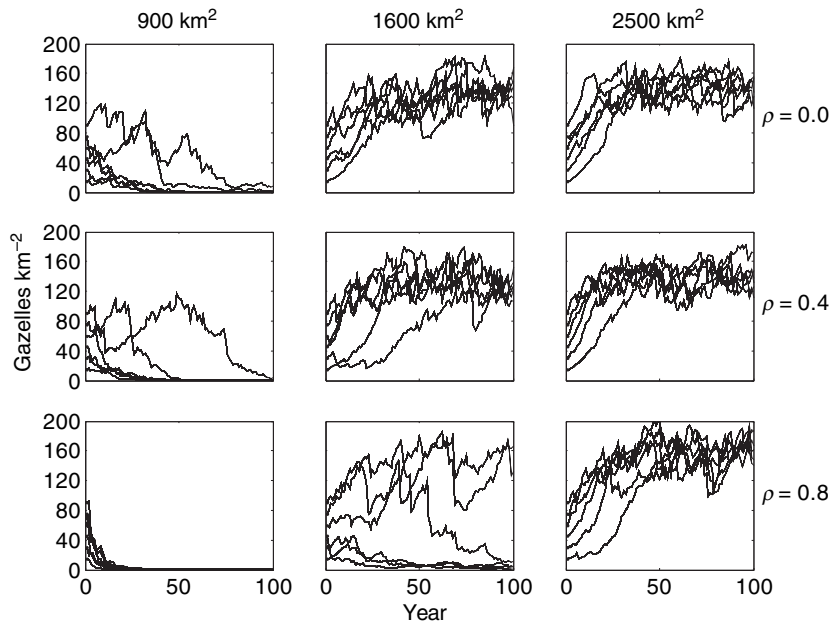
In the adaptive model used in most simulations, the probability of emigration  $\theta(V)$  is assumed to depend on the local daily rate of energy intake ( $Z[V]$ ) relative to the expected rate of daily energy gain averaged over the landscape  $E[Z(V)]$ . Following the marginal value theorem (Charnov 1976; Arditi & Dacorogna 1988), we use the following sigmoid threshold function (Fig. 1d):

$$\text{Probability of emigration: } \theta(V) = \frac{E[Z(V)]^\phi}{Z(V)^\phi + E[Z(V)]^\phi} \quad (10)$$

with the parameter  $\phi$  fitted by maximum-likelihood criteria to Thomson's gazelle data from Serengeti (estimated  $\phi = 2.9$  for 1995 data; estimated  $\phi = 1.8$  for 1996 data; the average value of 2.4 is used in our simulations) (Fryxell *et al.* 2004). Redistribution of Thomson's gazelles was deterministic, meaning that there was no variation in  $\theta(V)$  for a particular level of plant abundance. Our sense is that Thomson's gazelles usually have a rather diffuse herd structure, which would argue for this kind of representation. Pronounced stochasticity in herd movements, should they occur, would no doubt influence the probability of population persistence.

## RESULTS

We first evaluate the effect of landscape scale on persistence of gazelles ( $3 \times 3$  cells covering 900 km<sup>2</sup>,  $4 \times 4$  cells covering 1600 km<sup>2</sup>, and  $5 \times 5$  cells covering 2500 km<sup>2</sup>). In this set of simulations, we assume no spatial autocorrelation in rainfall. Our simulations suggest that Thomson's gazelles would be unlikely to persist on a lattice smaller than 16 cells covering 1600 km<sup>2</sup> (top row, Fig. 2), even though extinction might take a century to occur. The logical explanation for this is that in ecosystems of small spatial extent, Thomson's gazelles too infrequently experience intervals of positive growth to make up for the



**Figure 2** Simulated changes in population density (individuals  $\text{km}^{-2}$ ) over time for Thomson's gazelles for four alternate lattice sizes: ( $3 \times 3$  cells,  $4 \times 4$  cells,  $5 \times 5$  cells, and  $6 \times 6$  cells, each measuring  $10 \times 10 \text{ km}^2$ ) and three alternate degrees of spatial autocorrelation in rainfall ( $\rho = 0.0$ ,  $\rho = 0.4$ ,  $\rho = 0.8$ ). In each panel, six independent simulations are shown, each started at different initial densities of gazelles (ranging between 15 and 90 individuals  $\text{km}^{-2}$ ). Each simulation was based on a different stochastic rainfall series. Each simulation assumed that animals used an energy-matching strategy to move between cells on the lattice.

inevitable periods of decline. Once a model population has declined to low densities, consumers are less able to maintain vegetation as a nutritious grazing lawn for an extended part of the growing season (McNaughton 1984; Hobbs & Swift 1988; Fryxell 1991), accelerating the extinction vortex. A more detailed mathematical explanation for this kind of threshold extinction effect in grazing systems with hump-shaped fitness functions (albeit in a non-spatial framework) is presented in Van de Koppel *et al.* (1996).

We repeated our analyses for varying degrees of positive spatial autocorrelation in rainfall (correlation coefficient  $\rho = 0.4$  and  $0.80$  for adjacent cells), but maintaining the observed gradient in rainfall from north to south in the model system. This allows us to test the degree to which spatial independence in resource variability is implicated in consumer persistence. A correlation coefficient of  $\rho = 0.8$  is most consistent with the available rainfall records for the Serengeti Plains (Norton-Griffiths *et al.* 1975).

Our simulations predict that for landscapes of limited extent, mean gazelle abundance should tend to decline with increasing levels of spatial autocorrelation in rainfall (middle and bottom rows, Fig. 2), accompanied by increased risk of extinction. However, model populations of gazelles can persist even under high levels of spatial autocorrelation in rainfall, provided that they have free access to areas over  $1600 \text{ km}^2$ . Hence, unrestricted access to open grasslands of large spatial extent is needed to avoid extinction over the next 100 years for Thomson's gazelles in Serengeti.

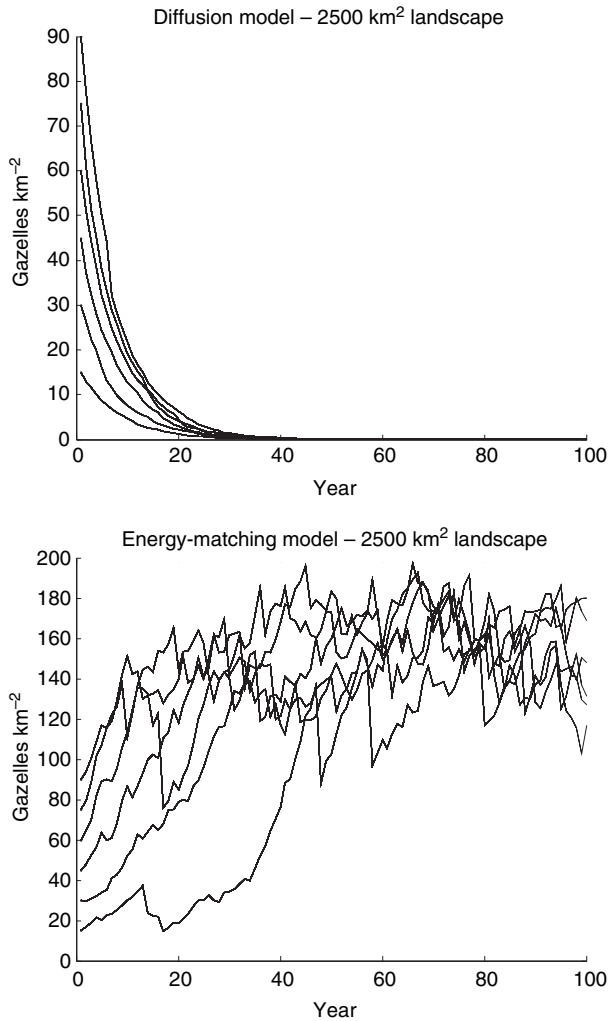
The mean density of Thomson's gazelles recorded over 16 censuses in 1995 and 1996 was  $78 \text{ individuals km}^{-2}$ . For

large landscapes ( $2500 \text{ km}^2$ ) and realistic levels of spatial autocorrelation in rainfall ( $\rho = 0.8$ ), our model predicts levels of gazelle abundance ( $120\text{--}180 \text{ individuals km}^{-2}$ ) that are somewhat higher than these field estimates (Fig. 3), but certainly in the right ballpark. Competition with other grazing herbivores could readily explain the discrepancy between observed densities and those produced by our model.

In another set of simulations, we relaxed our assumption that animals efficiently locate neighbouring patches offering the most favourable level of resource abundance. We apply a behavioural model with a constant rate of gazelle dispersal and uniform redistribution among neighbouring patches, analogous to a pure diffusion process (Turchin 1998). Outcomes of the pure diffusion model invariably lead to gazelle extinction (Fig. 3), emphasizing the importance of adaptive decision-making for long-term viability of Thomson's gazelles.

## DISCUSSION

Almost all of the parameters used in these models have been estimated experimentally or from data on the spatial distribution of gazelles in Serengeti (McNaughton 1985; Wilmshurst *et al.* 1999; Fryxell *et al.* 2004). Hence, we think that the simulation results are reasonably robust. Nonetheless, we did estimate the maximum rate of increase and the mortality rate of gazelles when food is sparse from allometric relationships, assumptions that are perhaps debatable. Extensive demographic research would be needed to estimate these final parameters, work which is beyond the scope of the current study.



**Figure 3** Simulated changes over time for Thomson's gazelles for two alternate behavioural models. In the top panel, a fixed proportion of gazelles emigrate from each cell each day, whereas in the bottom panel, gazelles follow an energy-matching emigration strategy. The energy-matching strategy is most consistent with the Serengeti data (Fryxell *et al.* 2004). In each panel, six independent simulations are shown, each started at different initial densities of gazelles (ranging between 15 and 90 individuals  $\text{km}^{-2}$ ). Each simulation was based on a different stochastic rainfall series and each assumed a high degree of spatial autocorrelation in rainfall ( $\rho = 0.8$ ).

In the absence of definitive information to the contrary, we made the conservative decision to make the maximum rate of increase and the maximum rate of decline of similar magnitude. There is some evidence from other systems, such as Soay sheep on St Kilda (Clutton-Brock & Pemberton 2004) that rates of ungulate decline may be faster than rates of increase. If this proves to be true of Thomson's gazelles as well, this would further decrease the probability of persistence.

We assumed that gazelles feed indiscriminately, which is probably true at low levels of resource abundance, but probably underestimates the effect of selective feeding for the highest-quality tissues (leaf and leaf sheath) that no doubt occurs at high levels of resource abundance. In the absence of information on feeding selectivity by Thomson's gazelles, a notoriously difficult process to measure, we considered it wiser to assume non-selectivity.

An additional factor that we ignore in this paper is the role of competition and/or facilitation with other herbivore species. The Serengeti Plains also support large numbers of other herbivores, such as zebra, wildebeest, hartebeest, topi, eland, and Grant's gazelles. Depending on the densities and spatial distribution of other species, feeding conditions for Thomson's gazelles may be improved or diminished by their presence. For simplicity, we have chosen to ignore these inter-specific interactions in this paper, but plan to address this issue in future publications. We maintain that understanding of spatially-explicit food-webs is best served by considering simple trophic modules (one consumer species, one resource) in isolation, before linking different species together in a community model. At this stage, we do not know as much about consumption and within-season movement patterns by other herbivores as we do for Thomson's gazelles, further restricting our ability to adequately model the full food web.

We have represented the plant component in an admittedly simplistic fashion. Real savannah plant communities are composed of many different grasses and forbs, each of which may have different growth dynamics and qualitative changes with maturation. Our experience in Serengeti grasslands, however, suggests to us that growth of most plant species in the sward tends to be pretty synchronous during the wet season. Spatial variation in soil conditions tends to create substantial local heterogeneity in resources, as does variation in size structure among individual herbivores at a particular site. We are still a long way from being able to model multiple grass species and mixtures of plant tissue types, even for a system as well-studied as Serengeti. We would submit that our model may be somewhat more 'realistic' than many others in the literature, in that subsidized re-growth from below-ground reserves is more defensible for perennial grasses and forbs than the more typical assumption of pure logistic plant growth. Clearly this is an area in urgent need for further study.

In spite of these simplifications, our model does a reasonable job of recreating spatial dynamics (Fryxell *et al.* 2004) and mean abundance of Thomson's gazelles in Serengeti, without any fitting to demographic time-series data. This suggests that we have captured at least some of the salient features important to their trophic dynamics. No doubt other modelling frameworks, such as use of age-specific difference equations to model gazelles of different

age, might illuminate other important features of gazelle ecology.

Temporal variability in rainfall is a well-described feature of Serengeti National Park. The rain that does fall tends to vary to some degree in different regions of the Park, but tends to be similar within the plains region (Norton-Griffiths *et al.* 1975). As a result of uneven rainfall, no patch is likely to sustain animals permanently, so movement of some kind is essential to long-term persistence. Because of spatial autocorrelation in rainfall in Serengeti, this requires a substantial area.

There is a narrow range of conditions when gazelles are in positive energy balance (Wilmshurst *et al.* 1999), because of trade-offs between vegetation quality and abundance at different stages of grass growth. Tall pastures provide ample food, but of poor quality, whereas short pastures offer less abundant food, but of higher quality. Hence, Thomson's gazelles prosper best when food is neither too common, nor too sparse (Wilmshurst *et al.* 1999). When grass biomass climbs above the optimum the fitness of gazelles is compromised. Growing swards can rapidly decline in quality, such that they are no longer profitable to grazing gazelles. As a consequence, there is strong selection for adaptive patterns of patch departure and redistribution amongst neighbouring patches. Movement decisions need not be perfect to achieve persistence, at least in Thomson's gazelles, but they must be considerably better than simple diffusion.

Our models suggest that adaptive movement across a complex ecological landscape is essential in maintaining Thomson's gazelles in the face of seasonal and spatial variation in grass abundance. The implications arising from this depend on the spatial scale at which there is meaningful heterogeneity in vegetation abundance. In Serengeti, plant abundance tends to be rather uniform over large areas, so Thomson's gazelles require unrestricted access to large expanses of savannah grassland. If this proves to be true for other species or other ecosystems, this would be difficult to reconcile with human land use priorities. Other systems may have sufficient vegetation heterogeneity at a local scale to sustain herbivores in much smaller reserves. Regardless of the spatial scale at which vegetation heterogeneity occurs, however, understanding of complex behavioural responses to spatially and temporally heterogeneous food supplies may be essential to successful conservation of grazing herbivores.

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