

PREDICTIVE MODELS OF MOVEMENT BY SERENGETI GRAZERS

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Abstract. Many animal species are unevenly distributed across the landscape, in spatial patterns that continually shift over time. Such a shifting mosaic is thought to have profound implications for the persistence and stability of ecosystems. Management and conservation of natural systems would be enhanced if we could accurately predict movement. Such prediction has not yet been possible. Here we use an extensive set of field data on food abundance and quality, combined with experimentally derived measures of nutritional value, to predict the spatial distribution of Thomson's gazelles (*Gazella thomsoni thomsoni* Günter) on the Serengeti Plains of East Africa. Twelve plausible models, based on alternate foraging objectives or movement rules, were assessed against field data on food and grazer abundance gathered at biweekly intervals (every two weeks) over the course of the wet seasons in two different years. Nomadic movements of gazelles closely tracked changes in the spatial distribution of short grass swards. Gazelles left short grass patches when local daily energy intake dropped below the expected intake averaged across the landscape. Subsequent redistribution of gazelles among neighboring patches was proportional to daily rates of energy intake in each patch. Thus, nomadic movements by Thomson's gazelles were predictable on the basis of local energy gain. This suggests that adaptive behavioral models can provide useful predictive tools for understanding the dynamics of complex natural systems.

Key words: adaptive behavior; East Africa; energy intake rate; foraging; functional response; *Gazella thomsoni*; nomadic movement; predictive models; Serengeti; short grass; Thomson's gazelle.

INTRODUCTION

Although the ecological consequences of animal movement across heterogeneous landscapes recently have received much attention, empirical evidence for their underlying biological causes remains elusive (Kareiva and Odell 1987, Turchin 1998). This stems from weak linkages between models and appropriate field data, and the logistic difficulty of sampling animal locations and predictor variables at large spatial scales.

Such limitations apply to large-mammal grazing systems, where grasslands exhibit a complex mosaic of grass heights, species composition, and abundance per unit area (Turner et al. 1993, 1994, Bailey et al. 1996, Bradbury et al. 1996, Farnsworth and Beecham 1999). Although much is known about the mechanics of grazer physiology and feeding behavior, we do not yet know whether feeding choices at the local scale determine herbivore movements and distribution patterns occurring at the larger landscape scale (Turner et al. 1993, Bailey et al. 1996, Farnsworth and Beecham 1999). If feeding choice determines large-scale movements, then one could use such measures to manage ecosystems supporting large, mobile populations of herbivores and

the predators that feed on them (Sinclair and Arcese 1995). Here we show how adaptive behavioral models can be applied to understand the dynamics of complex natural systems (Sutherland 1996, Fryxell and Lundberg 1998).

To address this problem, we linked behavioral modeling with observational studies of the spatial distribution of Thomson's gazelles in Serengeti National Park, Tanzania (Wilmshurst et al. 2000; see Plate 1) and experimental feeding studies of captive Thomson's gazelles, *Gazella thomsoni thomsoni* (Wilmshurst et al. 1999). Wilmshurst et al. (2000) sampled the spatial distribution of gazelles every 1 km from biweekly (once every two weeks) transects 220 km in length, along a series of tracks within a 40 × 40 km grid centered on the northwestern Serengeti plain (coordinates of northwestern corner: 2°32.1' S, 34°57' E). Eight transects each year were driven during the wet seasons of 1995 and 1996.

The gazelle census data (Fig. 1) demonstrate two features: (1) large spatial disparity in grazer abundance at any point in time [local densities spanning 0–300 gazelles per km²], and (2) rapid changes in the location of peaks and troughs over time. These changes reflect gazelle movements, because the time between censuses was far too short to detect substantial population changes due to births or deaths. At the same locations used to estimate gazelle abundance, we also sampled food

Manuscript received 16 January 2004; revised 16 March 2004; accepted 23 March 2004. Corresponding Editor: G. M. Henebry.

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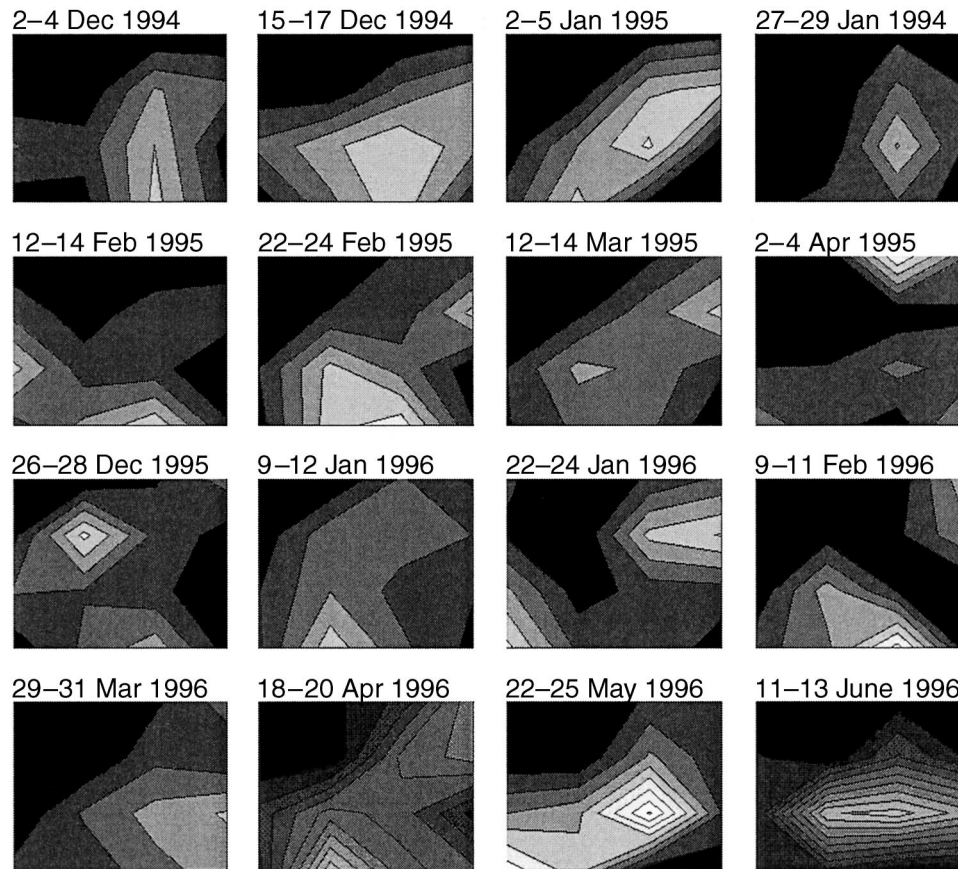


FIG. 1. Sequential censuses (taken once every two weeks) of spatial distribution of Thomson's gazelles within a 40×40 km grid centered on the northwestern Serengeti Plain (coordinates of northwestern corner: $2^{\circ}32.1' S$, $34^{\circ}57' E$). Shading corresponds to gazelle density, with the darkest shade being close to 0 and lightest shade close to 300 animals/km².

abundance (in grams per square meter) and digestible energy content (our measure of food quality, measured in megajoules per gram). This information was translated into rates of gain of dry matter or energy, based on mechanistic foraging models parameterized for captive animals in an independent series of controlled experiments (Wilmschurst et al. 1999). These mechanistic models are described mathematically in the *Foraging and Movement Models* sections that follow. Using information theoretic methods, we evaluated the ability of each alternative behavioral model to predict the shifting mosaic of Thomson's gazelles.

FORAGING MODELS

The first set of five models related to foraging objective. Grazers might select areas that provide the most rapid hourly intake of dry matter or energy. Alternatively, animals could integrate foraging gains over a longer time frame, preferring to graze in locations where they could acquire the most dry matter or energy per day. We compared these four alternatives (hourly food intake, hourly energy intake, daily food intake, and daily energy intake) with a null model that the

spatial distribution of gazelles was unrelated to food or energy intake.

Experimental data (Wilmschurst et al. 1999) on gazelle grass consumption (in kilograms per hour) were fitted to the Michaelis-Menten equation for the short-term functional response:

$$\text{hourly food intake model, } X(V) = \frac{aV}{b + V} \quad (1)$$

where a is the maximum (i.e., asymptotic) rate of forage consumption (measured in kilograms per hour), b is the grass biomass (in grams per square meter) at which intake is one-half of the maximum rate, and V is vegetation biomass (in grams per square meter). In the absence of any other constraints, animals would gain the highest rate of dry matter food intake by maximizing the functional response, $X(V)$.

Energy intake was estimated by multiplying hourly consumption ($X[V]$) by a linear function describing the digestible energy content of forage ($Q[V] = c - dV$), where c is the maximum forage quality and d is the rate at which quality declines with plant biomass, based on the experimental data of Wilmschurst et al. (1999).

This yielded the following function for hourly energy intake:

$$\text{hourly energy intake model, } Y(V) = \frac{aV(c - dV)}{b + V}. \quad (2)$$

One cannot simply multiply Eq. 2 by the daily foraging time to estimate the daily rate of energy intake. 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 (Fryxell 1991, Illius and Gordon 1992, Wallis de Vries 1996, Prins and Olf 1998, Wilmshurst et al. 1999, 2000). Modeling this effect required a second, digestive constraint: ad libitum consumption as a function of plant biomass ($I(V)$). Field measurements indicated that digestible energy content of the sward declined with sward biomass in an approximately linear fashion (Wilmshurst et al. 1999). We therefore modeled the digestive constraint (in megajoules per day) by the function $I(V) = (e - fV)$, where e is the maximum daily intake of energy and f is the rate at which daily intake declines with sward biomass. Daily energy gain was calculated accordingly (Fryxell 1991, Wilmshurst et al. 1999) by taking the lesser of the constraint functions $I(V)$ or $Y(V)t_{\max}$, where t_{\max} is the maximum number of hours spent foraging each day:

$$\begin{aligned} &\text{daily energy intake model, } Z(V) \\ &= \min \left\{ \frac{aVt_{\max}(c - dV)}{b + V}, e - fV \right\}. \quad (3) \end{aligned}$$

The daily rate of food intake can be calculated similarly as the minimum of the following constraints:

$$\text{daily food intake model, } W(V) = \min \left\{ \frac{aVt_{\max}}{b + V}, \frac{e - fV}{c - dV} \right\}. \quad (4)$$

With parameters predicting foraging rates and energy gain by gazelles and energy content of grass swards in relation to their abundance for each of the models, we predicted the rate of energy or food intake in relation to categories of grass biomass (termed "grass bins"). Model parameters are listed in the legend to Fig. 2. We numerically integrated food intake or energy gain over each bin spanning 10 g/m². After correcting for mean gazelle density in each census, we estimated the linear relationship between corrected gazelle density in each grass category and the rate of food or energy intake in that grass category. We also tested a null model, assuming no consistent variation in gazelle density in relation to grass abundance. We evaluated the predictive ability of the resulting five foraging objective mod-

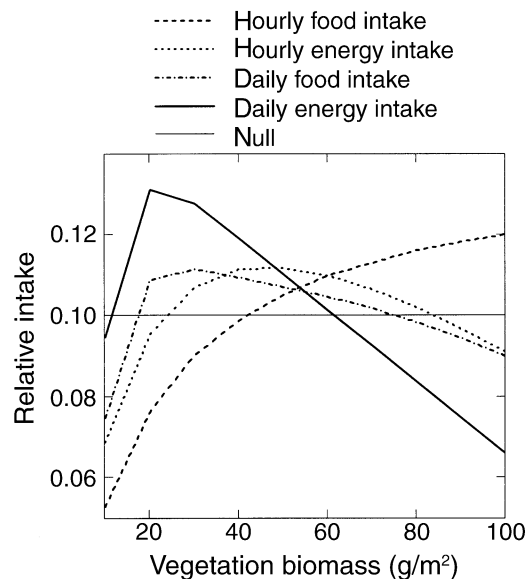


FIG. 2. Relative gazelle fitness due to food or energy intake (over the grass biomass range 0–100 g/m²) predicted by the four foraging models and the null model (parameters: $a = 0.38$ kg/h, $b = 16$ g/m², $c = 11.201$ MJ/kg eaten, $d = 0.05$ MJ/kg eaten per gram of grass, $e = 22.7$ MJ/day, $f = 0.13$ MJ/day per gram of grass). For explanation of parameters, see *Foraging models*. Relative ecological fitness was estimated by dividing intake at a given grass biomass by intake summed over the full range (10–100 g/m²).

els using Akaike's information criteria (AIC_c), corrected for small sample size (Burnham and Anderson 1998), comparing observed gazelle density with that predicted by the model. This approach evaluates the likelihood of each candidate model relative to the number of parameters fitted from the data, with low values of AIC_c indicative of the most plausible models. We then calculated the difference in AIC_c scores between each model and the best model and used ΔAIC_c to score their relative performance.

Our models predicted substantially different patterns of relative fitness (as measured by food intake or energy intake) with respect to grass abundance (Fig. 2). The model of daily energy intake predicted a unimodal distribution of relative intake, with a maximum value at a slightly lower level of food abundance (20 g/m²) than the model of daily food intake (30 g/m²). The model of hourly energy intake predicted a maximum value at 50 g/m² grass biomass. The model of hourly food intake predicted a maximum at the highest levels of food abundance, here truncated at 100 g/m². Hence, the models made different predictions for the grass biomass where gazelles would be found in greatest abundance.

We compared the observed gazelle distribution with these predictions. Gazelles did not simply concentrate at sites where food was most abundant. Instead, they concentrated on grass swards of low biomass, with a maximum value at a grass biomass of 20 g/m² (Fig. 3). Variation in gazelle population density was best pre-

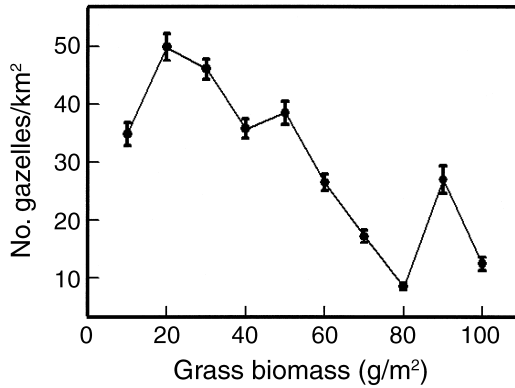


FIG. 3. Densities (mean \pm 1 SE) of adult Thomson's gazelles on the Serengeti Plains over 16 censuses during 1995–1996 in relation to grass biomass.

dicted by daily energy intake (Fig. 4). The hourly food intake model was the second best predictor of gazelle density from census to census ($\Delta AIC_c = 7$), but the best-fit model implied that gazelles go where hourly food intake is lowest, which is mechanistically implausible. The other foraging models were poor predictors of gazelle densities ($\Delta AIC_c = 25$ –28). The observed distribution of gazelle clearly supports the energy-maximizing model, which predicts that gazelles should favor short grasslands (20 g/m²) whenever available.

MOVEMENT MODELS

Having determined that daily energy intake best describes the sward preferences by Thompson's gazelles, we evaluated the following seven movement models by which gazelles might redistribute themselves across the landscape.

Model 1.—Animals might have a constant probability of dispersal from a given patch (estimated by maximum likelihood from the census data) and a uniform probability of relocating into each neighboring patch. This was our null movement model.

In all of the other six models, individuals base the probability of emigration on local energy intake compared to expected energy intake over the entire landscape, but use different rules for redistribution of emigrants.

Model 2.—Individuals have a uniform probability of relocation into neighboring patches (termed the local uniform model).

Model 3.—Individuals move to the best neighboring patch (termed the local optimal model).

Model 4.—Individuals immigrate into each neighboring patch with a probability proportionate to energy gain (termed the local matching model).

Model 5.—Individuals immigrate with uniform probability into all patches in the landscape (termed the global uniform model).

Model 6.—Individuals immigrate into the best neighboring patch in the entire landscape (termed the global optimal model).

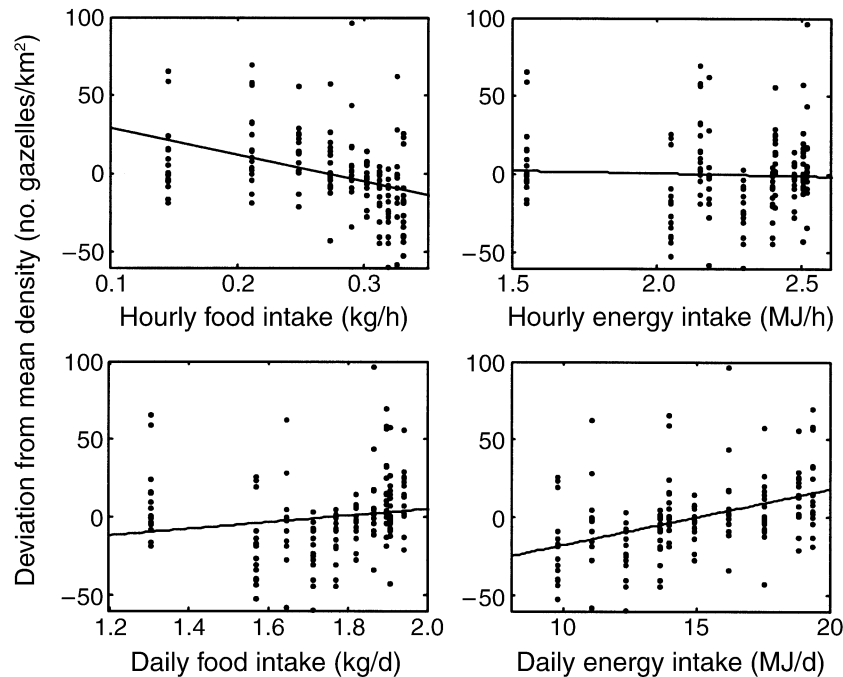


FIG. 4. Local variation in Thomson's gazelle density (corrected for census-specific mean density) in relation to four alternative intake models.



PLATE 1. (Left) A mixed herd of Thomson's gazelles on the Serengeti Plains at the beginning of the wet season. (Right) Long-distance shot showing a localized rainstorm on the Serengeti Plains. Photo credit: J. Fryxell.

Model 7.—Individuals immigrate into all patches in the landscape with a probability proportionate to energy gain (termed the global matching model).

We evaluated the predictive ability of the seven movement models using Akaike's information criteria (AIC_c), corrected for small sample size (Burnham and Anderson 1998), comparing observed gazelle density in each grid cell (Fig. 1) with that predicted by the model.

To evaluate the movement models, we used a 4×4 spatial lattice model to mimic the 4×4 spatial lattice used to summarize gazelle censuses (Fig. 1). Movements of gazelles across the lattice were modeled with a daily time step, for a 112-day growing season, corresponding to a series of eight biweekly (once every two weeks) censuses. Gazelles were uniformly distributed on day 1 in the models, at an average density taken from the first census in each year. Thereafter, cell-specific grass abundance actually observed at biweekly intervals was used to determine probabilities of emigration from each cell and the corresponding probability of immigration into each cell according to the different behavioral rules outlined earlier.

The probability of emigration $\theta(V)$ in models 2–7 was predicted on the basis of a sigmoid threshold function of local daily energy gain ($Z[V]$) relative to the expected rate of daily energy gain averaged over the landscape $E(Z[V])$

$$\text{probability of emigration: } \theta(V) = \frac{E(Z[V])^\phi}{Z[V]^\phi + E(Z[V])^\phi} \quad (5)$$

with the parameter ϕ fitted by maximum likelihood criteria to the Serengeti data (estimated $\phi = 2.9$ for 1995 data; estimated $\phi = 1.8$ for 1996 data).

Eq. 5 was deemed necessary because animals often exhibit partial foraging choices that approximate step functions by smooth sigmoid functions (Fryxell and Lundberg 1998). Had Serengeti gazelles made a unan-

imous choice about departure, one would anticipate that the fitted value of ϕ would have been much higher, given that $\phi = \infty$ implies perfect choice. Such parameter fitting is a normal component of formal model evaluation (Burnham and Anderson 1998).

How do gazelles achieve a high daily energy gain? Gazelle movements were best predicted by the local matching model, in which the probability of emigration from a given patch and the probability of immigration into neighboring sites were determined by relative rates of energy intake. The other local models were poorer at predicting spatial patterns of gazelle distribution (local uniform model: $\Delta AIC_c = 25$, local optimal model: $\Delta AIC_c = 374$). Global models performed worse than local models in predicting changes in gazelle distribution from census to census (global uniform model, $\Delta AIC_c = 36$; global matching model, $\Delta AIC_c = 25$; global optimal model, $\Delta AIC_c = 617$). The null model (using a best-fit coefficient of daily diffusion = 0.01) also performed poorly relative to the best behavioral model ($\Delta AIC_c = 92$). The gazelle distribution data were clearly most consistent with a model in which both the probability of emigration from a given patch and the probability of relocating into neighboring patches depended on daily energy intake.

DISCUSSION

The Serengeti census data for Thomson's gazelles (Fig. 1) showed considerable spatial variation in abundance at any point in time and rapid changes in the location of peaks and troughs over time. Both are diagnostic features of a shifting mosaic. The available empirical evidence is most consistent with the hypothesis that movements of Thomson's gazelles from patch to patch depended on their daily rate of energy intake matched against that in neighboring sites. This result is consistent with previous theoretical predictions that short grass swards of relatively low biomass should offer the highest energetic rewards for grazing

ungulates (McNaughton 1984, Fryxell 1991, Wallis de Vries 1996, Prins and Olff 1998). Our result extends to the landscape scale similar results from several small-scale experiments that foraging rates and patch preferences are proportional to daily energy intake (Langvatn and Hanley 1993, Wilmshurst and Fryxell 1995, Wilmshurst et al. 1995, Wallis de Vries et al. 1999).

Previous theoretical models have suggested that complex spatial distribution of grazers and their food resources can readily arise via simple rules for foraging and movement (Arditi and Dacorogna 1988, Turner et al. 1993, Farnsworth and Beecham 1999). Rarely, however, have field researchers tried to evaluate movement by free-ranging animals in relation to local food conditions. Like the pioneering study of Focardi et al. (1996), our results suggest that animals respond to local variation in food supplies relative to the expectation over entire the landscape in making decisions about whether to use a given spatial location. Our models are at a much larger spatial scale, however, than those of Focardi et al. (1996) and there are other important differences in the underlying basis of the foraging constraints and movement rules. We see much promise in linking mechanistic movement models (i.e., based on correlated random walks) with behavioral responses to variation in food resources at varying spatial scales (Focardi et al. 1996, Farnsworth and Beecham 1999). Formal model evaluation of the kind described here provides a powerful tool to develop such models.

Earlier work, at a coarser spatial scale, has shown that soil characteristics and local nutritional quality of plants influence the spatial distribution of Serengeti grazers (Hobbs and Swift 1988, McNaughton 1988, Bergman et al. 2001). The sheer magnitude of our sampling regime (some 3500 observation points) precluded detailed nutrient analysis to augment the energetic analysis. Previous studies have shown, however, that energy-optimizing patch choice strategies often optimize intake of critical nutrients (Wilmshurst and Fryxell 1995). Water availability also can influence the spatial distribution of grazers in semiarid African systems (Western 1975, Redfern et al. 2003). Previous aerial survey work has demonstrated that water availability is rarely limiting, however, to Serengeti grazers during the wet season (Maddock 1979), especially Thomson's gazelles, so this seems to be an unlikely alternate explanation for the observed shifting distribution.

Our results show how Thomson's gazelles distribute themselves at a fine spatial scale according to energy gain, with proportionately more animals in patches with swards of low grass biomass, as predicted by the energy-matching model. Our study is unusual in the close matching of our predictions to the observed movements at an ecologically realistic spatial scale. This approach suggests that energetic models with appropriate param-

eter estimates can predict the shifting mosaic of organisms across complex spatial landscapes.

In a companion paper (J. Fryxell, J. F. Wilmshurst, A. R. E. Sinclair, R. D. Holt, P. A. Abrams, and D. T. Haydon, *unpublished manuscript*), we show that adaptive movements by Thomson's gazelles are essential to long-term viability. This suggests that adaptive patterns of patch selection help to sustain nomadic grazer populations in the face of seasonal and spatial variation in grass abundance. Mobile species, such as Thomson's gazelles, accordingly require unrestricted access to large expanses of savannah grassland. Moreover, adequate understanding of complex behavioral responses by grazers to spatially and temporally heterogeneous food supplies may be essential to successful conservation.

ACKNOWLEDGMENTS

We thank the Natural Sciences and Engineering Research Council of Canada for financial support of the Serengeti field study. This work was conducted as part of the Serengeti Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-94-21535), the University of California at Santa Barbara, and the State of California. We thank Dan Haydon, Peter Abrams, Bob Holt, Geoffrey Henebry, and two anonymous referees for critical comments on an earlier draft of the manuscript.

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