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**Ricardo M. Holdo, Robert D. Holt, and John M. Fryxell. 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications* 19:95–109.**

Appendix A. Savanna dynamics model equations and their derivation, including a table of state variables and model parameters.

Appendix A. SD model equations and their derivation. The full model incorporates submodels for each of the key system components and interactions shown in Fig. 2 of the main text.

*Grass dynamics.* — The submodel for grass dynamics has to incorporate a number of processes: production as a function of rainfall, the inhibitory influence of senescent biomass, fire, competition with trees, and herbivory. In each cell of the model lattice, two grass compartments are simulated: green or live ( $G$ ) and dry or senescing ( $D$ ) grass. The equations are given by:

$$\Delta G = r_{max}(t)(G + \sigma) \left( 1 - \frac{G + \rho D}{K_G} \right) - \delta_G(t)G - \frac{I_G^W W + I_G^E E}{g} - p(t)G \quad (\text{A.1})$$

and

$$\Delta D = \delta_G(t)fG - \delta_D D - \frac{I_D^W W + I_D^E E}{g} - \tau \frac{W}{g} p(t)D \quad (\text{A.2})$$

The terms of Eq. A.1 are growth, decay, consumption by herbivores, and losses to fire. The terms of Eq. A.2 are input from the decay of green grass, and decomposition, consumption, trampling, and losses to fire.  $W$  and  $E$  are wildebeest and elephant population density, respectively,  $g$  is the proportion of the cell occupied by grass, and  $p(t)$  is the proportion of the cell that burns at time  $t$ . As  $g$  declines, the herbivores currently occupying the cell become increasingly concentrated on the portion of cell containing grass (i.e. population density  $\propto 1/g$ ), and grass consumption per unit area increases, leading to the terms  $W/g$  and  $E/g$  in Eqs. A.1 and A.2. Note that the model is implemented so that  $G$  and  $D \geq 0$ , and the various terms in Eqs. A.1 and A.2 are applied sequentially: *i.e.*,  $G$  and  $D$  are first updated with production and decay terms, followed by consumption, and finally, fire. If  $p(t) = 1$  for a given cell,  $G$  and  $D$  are zero at the start of the next daily time period.

*i. Grass production and decay.* Grass production is simulated by combining a grass growth model from Fryxell *et al.* (1988) with Owen-Smith's (2002) two-compartment model, fitted to

McNaughton's (1985) empirical equation for grass production as a function of rainfall. The two-compartment model allows two key effects to be incorporated: the suppression of new growth of  $G$  due to shading by  $D$  (Owen-Smith 2002) in ungrazed and unburned areas (which has the effect of reducing wildebeest intake and fitness in these areas), and the build-up of  $D$  over time, which fuels fires (Pellew 1983, Stronach and McNaughton 1989). As  $G$  dries up at the start of the dry season,  $D$  increases in biomass.

Both the maximum growth rate  $r_{max}$  and the grass carrying capacity  $K_G$  in Eq. A.1 are functions of annual rainfall (Fryxell *et al.* 2005),  $\rho$  represents the shading effect of  $D$  on  $G$ ,  $\sigma$  allows for aboveground growth when  $G = 0$  (permitted by the presence of belowground reserves (Fryxell *et al.* 1988)),  $\delta_G$  and  $\delta_D$  are decay rates, and  $f$  is the fraction of  $G$  that decays into  $D$  (we assume that some of  $G$  is lost directly as rapidly decomposed litter). Whereas  $D$  decays at a constant rate throughout the year, growth and decay of  $G$  depends on the season (McNaughton 1985). McNaughton (1985) found a strong sigmoidal relationship between annual rainfall  $R_{ann}$  and the length of the growing season ( $t_{grow}$ ) in the Serengeti, given by (Fryxell *et al.* 2005):

$$t_{grow} = 60 + \frac{300 \exp(R_{ann}/100)}{\exp(R_{ann}/100) + 518} \quad (\text{A.3})$$

We assume that  $r_{max}$  in Eq. A.1 depends linearly on daily rainfall  $R_{day}$  (McNaughton 1985) according to the equation

$$r_{max} = \psi R_{day} \quad (\text{A.4})$$

when  $t < t_{grow}$  (we assume that it is zero otherwise). Grass carrying capacity  $K_G$  is in turn linearly related to annual rainfall (McNaughton 1985) by the equation

$$K_G = \mu_0 + \mu_1 R_{ann} \quad (\text{A.5})$$

We assume that the decay rate  $\delta_G$  is 0 until the onset of the dry season, or the end of the growing season (whichever comes first, depending on rainfall according to Eq. A.3). We obtained a value

for  $\delta_G$  from McNaughton (1985), who provided an equation for conversion of  $G$  into  $D$  at the end of the wet season as a function of the initial value of  $G$  and rainfall; this results in a relatively invariant value of  $\delta_G$  across a wide rainfall gradient. We estimated the parameters  $\mu_0$ ,  $\mu_I$ ,  $\sigma$ , and  $\psi$  by fitting Eq. A.1 (minus the consumption and fire terms) to data on grass production (Fig. 2d in the main text), and  $\delta_D$  and  $f$  by fitting Eq. A.2 to data on accumulated necromass (McNaughton 1985) as a function of time since the last recorded fire (see Appendix B for more detail on the protocol used for estimating parameters).

*i. Tree-grass competition.* Within each lattice cell, the area that can be occupied by grass is reduced by competition from trees. Studies from a wide range of ecosystems with tree-grass mixtures, including the Serengeti (Metzger 2002), suggest that, as tree cover increases, grass biomass declines according to a negative exponential function (Jameson 1967, Walker *et al.* 1972, Burrows *et al.* 1990, Tapia *et al.* 1990, Scholes and Archer 1997). In the current implementation of the model we assume that trees are competitively dominant to grasses. In terms of the mechanics of the model, this means that as tree biomass increases, the proportion of a cell  $g$  that is occupied by grasses declines according to the function

$$g = g_0 \exp(-\theta C) \tag{A.6}$$

Here,  $C$  is tree canopy cover (between 0 and 1),  $\theta$  is a parameter that controls the rate of decay in grass biomass as a function of tree cover, and  $g_0$  represents the maximum amount of area that is covered by grass (Anderson and Talbot 1965, Sinclair 1979), and is included to account for reductions in grazing area caused by the presence of bare ground, rocks, rivers, etc. We estimated  $\theta$  from Serengeti plot data collected by Metzger (2002). In this data set,  $C$  quantifies the canopy cover of trees  $> 3$  m in height (Metzger, pers. comm.), so in the model,

$C = 10^{-4} \sum_{i=4}^6 n_i c_i$ , where  $n_i$  represents the number of trees per ha in height class  $i$ , and  $c_i$  is the

coefficient relating tree height to crown area.

iii. *Consumption by herbivores.* We assume that wildebeest feed on both high quality ( $G$ ) and low quality ( $D$ ) grass components, but that intake is higher for  $G$  than for  $D$ . We modeled intake as a combination of two constraints, a cropping constraint with a type II functional response, and a digestive constraint that sets an upper limit to daily voluntary intake  $dvi$  (Wilmshurst *et al.* 1999, Wilmshurst *et al.* 2000), resulting in the following equations for intake of green ( $I_G^W$ ) and dry ( $I_D^W$ ) grass in wildebeest, respectively:

$$I_G^W = \min\left(dvi_G, \frac{\alpha_w G}{\beta_w + G + D}\right) \quad (\text{A.7})$$

and

$$I_D^W = \min\left(dvi_D, \frac{\alpha_w D}{\beta_w + G + D}\right) \quad (\text{A.8})$$

In these equations,  $dvi_G$  and  $dvi_D$  are the maximum daily voluntary intakes of  $G$  and  $D$ , respectively. The parameter  $\alpha_w$  represents the cropping constraint, and  $\beta_w$  is the grass biomass at which intake is  $\frac{1}{2}$  of the maximum. We used an empirical equation relating maximum daily voluntary intake to forage %NDF (neutral detergent fiber) and animal mass derived by Wilmshurst *et al.* (2000) to estimate  $dvi_G$  and  $dvi_D$  for a 135-kg wildebeest, assuming for simplicity that  $G$  and  $D$  are of fixed quality and represent the lower (high quality) and upper (low quality) ranges of NDF for Serengeti grasses (obtained from Wilmshurst *et al.* 1999), respectively. We estimated the cropping constraint from an allometric equation derived by Shipley *et al.* (1994), and obtained  $\beta_w$  from Murray & Brown (1993). We also used allometric equations relating body mass with maximum intake (Shipley *et al.* 1994) and the half-saturation

parameter (Wilmshurst *et al.* 2000) to estimate  $\alpha_E$  and  $\beta_E$  for elephants. Given that elephants can survive on food of very low quality, we did not include a digestive constraint in the elephant intake equation.

In addition to removing grass through consumption, herbivores can contribute to biomass losses indirectly through trampling. This effect can be substantial in herbivore-dominated environments such as the Serengeti (Cumming and Cumming 2003). Since green grass is rapidly removed by consumption and decay each season, we introduced a trampling term only in the dry grass equation (Eq. A.2). We estimated the trampling parameter  $\tau$  for wildebeest from published values (Cumming and Cumming 2003).

iv. *Fire.* We treat fire as a stochastic binary process that depends on the occurrence of an ignition event ( $i$ ) and the fuel biomass ( $D$ ) available (McNaughton *et al.* 1988, Holdo *et al.* 2007). It has an expected value  $p_{burn}$  given by:

$$p_{burn} = i(t) \frac{\exp(g\kappa_1 D - \kappa_2)}{1 + \exp(g\kappa_1 D - \kappa_2)} \quad (\text{A.9})$$

We treat the probability of an ignition event as an externally driven independent variable, whereas fuel load is a dynamic variable (we assume that fire probability is independent of green grass biomass). In Eq. A.9,  $\kappa_1$  and  $\kappa_2$  are fitted parameters and  $g$  is the proportion of the cell occupied by grass. When  $t = t_{burn}$ ,  $i = 0$  when no fire occurs in the system and is  $i = 1$  when fire is present, and is 0 at all other times (for some simulations we give  $i$  a value of 0.5 to simulate semi-annual burning). Although we lack historic data on grass biomass in the Serengeti, we were able to estimate  $\kappa_1$  and  $\kappa_2$  (assuming annual ignition events) by fitting the model to data recording the extent of burning between 1960 and 2000 (Fig. 2f in the main text). The actual occurrence of fire in any given cell represents the realization of a Bernoulli process with expected value  $p_{burn}$ .

*Herbivore dynamics.* —The numerically-dominant mammalian herbivores of the Serengeti ecosystem are highly mobile. To understand their dynamics, we have to consider movement as well as local birth and death processes, as follows:

*i. Wildebeest movement.* Fryxell *et al.* (2004) showed that herbivores in the Serengeti move adaptively, reflecting the value of resources across the landscape. In SD, we assumed *a priori* that some measure of resource availability influences wildebeest movement choices, adopting the framework developed by Fryxell *et al.* (2004) for Thomson’s gazelles. The probability of emigration  $\Theta$  is given by:

$$\Theta = \frac{E(Z)^\varphi}{(Z)^\varphi + E(Z)^\varphi} \quad (\text{A.10})$$

The parameter  $\varphi$  in Eq. A.10 controls the shape of the migration function and  $Z$  equals resource availability in a cell. When  $\varphi > 1$ , this equation results in a switching response that is a function of local energy gain ( $Z$ ), relative to the expected gain averaged across the entire landscape [ $E(Z)$ ]. Elsewhere, we show that  $Z = gI_G^W N^q$ , where  $N$  is plant N content (Holdo *et al.*, submitted).  $Z$  can thus be viewed as a composite function that multiplies food quantity  $gI_G^W$  by a measure of food quality  $N^q$  to obtain an index of resource availability that maximizes wildebeest fitness. We assume that immigration  $\Omega$  into cell  $x$  due to emigration from cell  $y$  is equal to  $Z_x / \sum Z_i \Theta_{y,i}$ , provided that  $Z_x \geq Z_y$ , where  $\sum Z_i$  is the sum of  $Z$  over all cells for which  $Z_i \geq Z_y$ . Wildebeest that emigrate from a cell thus distribute themselves proportionately throughout the subset of target cells in the landscape that are of greater value than the cell they have left. We fit the SD model to monthly wildebeest distribution data for the entire GSE during the period August 1969-August 1972, driving the model with monthly rainfall data from this same period (Holdo *et al.*, submitted).

ii. *Local population dynamics.* Pascual *et al.* (1997) tested a number of alternative models of wildebeest population dynamics by fitting these models to census data. They concluded that models with constant recruitment and density-dependent mortality provide fits that are as good if not better than more complex models, so we chose to adopt such a model. Different functions have been used to model ungulate mortality as a function of resource availability: e.g., Michaelis-Menton (Hilborn and Mangel 1997, Pascual *et al.* 1997), hyperbolic (Owen-Smith 2002), and negative exponential (Fryxell *et al.* 1988). These all have the same qualitative form, so we chose a negative exponential function, resulting in the following wildebeest population growth equation:

$$\Delta W = \left[ b_w - m_w \exp\left(-a_w \frac{gI_G^W N^q}{W}\right) \right] W - \Theta + \Omega \quad (\text{A.11})$$

Here,  $b_w$  and  $m_w$  are the wildebeest birth and maximum mortality rates in a particular cell, respectively,  $a_w$  is a parameter that relates food resources per capita to mortality, and  $\Theta$  and  $\Omega$  are emigration and immigration rates between the cell and the rest of the lattice, respectively. We assume that the measure of resource availability that controls mortality equals that which controls movement, *i.e.*, the model is mechanistic in that wildebeest try to maximize their fitness by moving towards cells of relatively high food quantity and quality, and these same variables then control local population dynamics.

After fitting a wildebeest movement model (Holdo *et al.*, submitted), we were able to obtain estimates for  $b_w$ ,  $m_w$ ,  $a_w$ , by fitting the model to historical wildebeest census data by driving the model with rainfall data for the GSE for the period 1960-2001 (Fig. 3e in the main text, Appendix B). In the present version of the model, we maintain elephant population density at a constant value over time. We do this for two reasons. First, unlike the case of wildebeest, for

which we have a good understanding of density-dependent effects of food availability on population dynamics (Mduma *et al.* 1999), we lack data to parameterize an elephant numerical response function. Second, unlike wildebeest (Hilborn and Mangel 1997, pp. 199-200), elephant population numbers in the Serengeti have historically been largely determined by humans (mainly through poaching). Moreover, elephants live considerably longer than do wildebeest, and so their numbers will typically change much more sluggishly. We therefore treat elephant population density as an independent fixed parameter in the present paper. Further, we assume for simplicity that elephants are evenly distributed throughout the savanna habitat of the ecosystem. Our model is thus semi-dynamic in terms of the herbivore populations. Among future extensions of the model that we contemplate will be an inclusion of elephant dynamics.

*Tree dynamics.* —Pellew (1983) gathered an extensive amount of data on growth rates, fire effects, and elephant damage on *Acacia tortilis* and other species in the Seronera area of the Serengeti, and used these data to parameterize a model of tree population dynamics as a function of fire and browser population density. With minor modifications, we have adopted Pellew's model to simulate tree dynamics in SD. We used *A. tortilis* as a model tree for the system, given its spatial ubiquity and numerical dominance throughout much of the Serengeti (Pellew 1983). Pellew's model is size-structured, with six tree height classes (0-1, 1-2, 2-3, 3-4, 4-6, and > 6 m). He used field observations to obtain parameters for fire and elephant damage and growth as a function of height (Pellew 1983). We adapted Pellew's model as a matrix submodel in SD, with an annual time step and density-dependent growth and recruitment. In the submodel, trees are first exposed to elephant herbivory, followed by fire, growth, and recruitment, as follows.

Elephant damage is represented by two matrices  $\mathbf{E}_1$  and  $\mathbf{E}_2$  (given in Appendix C). The default coefficients of  $\mathbf{E}_1$  and  $\mathbf{E}_2$  are based on an estimated elephant population density of 0.2

elephants  $\text{km}^{-2}$  in Seronera during the 1970s (Pellew 1983). In our model simulations, we assumed that departures in elephant population density from this default value lead to proportional changes in the coefficients.  $\mathbf{E}_1$  and  $\mathbf{E}_2$  are used to generate a vector of trees that revert to smaller size classes  $\mathbf{r}_E$ , and a vector of undamaged trees  $\mathbf{u}_E$ , as follows:

$$\mathbf{r}_E = \mathbf{E}_1 \mathbf{n}(t) \quad (\text{A.12})$$

$$\mathbf{u}_E = \mathbf{n}(t) - \mathbf{E}_2 \mathbf{n}(t) \quad (\text{A.13})$$

Here,  $\mathbf{n}(t)$  is the vector of tree size classes in given cell at time  $t$ . Fire then affects those trees that have escaped elephant damage, producing two vectors: trees that have reverted to smaller size classes following fire ( $\mathbf{r}_F$ ) and trees that have escaped both elephant and fire damage ( $\mathbf{u}_F$ ):

$$\mathbf{r}_F = \mathbf{F}_1 \mathbf{u}_E \quad (\text{A.14})$$

$$\mathbf{u}_F = \mathbf{u}_E - \mathbf{F}_2 \mathbf{u}_E \quad (\text{A.15})$$

$\mathbf{F}_1$  and  $\mathbf{F}_2$  are fire damage matrices (given in Appendix C). The vector of trees at  $t+1$  is equal to the sum of trees that grow and establish from the undamaged population, plus those trees that have reverted to smaller size classes:

$$\mathbf{n}(t+1) = \mathbf{G} \mathbf{u}_F + \mathbf{r}_E + \mathbf{r}_F \quad (\text{A.16})$$

$\mathbf{G}$  is the growth and recruitment transition matrix (given in Appendix C). Recruitment occurs as a result of seedling establishment from seeds produced by the largest size class (Pellew 1983).

Recruitment and growth are density-dependent and limited by the carrying capacity of each cell.

A meta-analysis conducted by Sankaran *et al.* (2005) showed that maximum canopy cover in savannas increases with rainfall, saturating at about 80% cover. This yields a tree carrying capacity  $K_T$  equal to 400 trees  $\text{ha}^{-1}$  in our model if we assume an average crown area of 20  $\text{m}^2$  for the 6-m height class (see below). We added logistic-like density-dependence to the model by multiplying the growth coefficients ( $g_{ij}$ ) of matrix  $\mathbf{G}$  (given in Appendix C) by  $(1 - n_6/K_T)$ , where

$n_6$  is the mature size class. Pellew (1983) argued that by the time a seedling is fully established, natural spacing due to intra-specific competition has already occurred, and little further competition occurs until maturity (height > 6 m). At this stage, trees escape giraffe browsing and their canopies expand. Since *A. tortilis* has a low shade tolerance (Pellew 1983), we assume that immature classes suffer reduced growth as the mature tree canopy expands, and thus density-dependent growth limitation is due only to the largest size class  $n_6$ . To model recruitment limitation, on the other hand, we assume that *all* size classes limit the ability of seedlings to become established, so the coefficient  $s$  (the per capita rate of seedling recruitment, see matrix **G** in Appendix C) is multiplied by  $(1 - \sum_i n_i / K_T)$ . Pellew (1983) was unable to provide a reliable estimate for the rate of seedling recruitment as a function of the number of mature trees, so we fitted a value of  $s$  by running the model over an 8-year period between 1971-78 for which initial and ending tree height distributions, the fire regime and elephant population density were known in the system. We adopted the value of  $s$  that maximized the fit between the 1978 model size class distribution and the data. To estimate the amount of woody cover represented by a particular size distribution  $\mathbf{n}$ , (for model output and to estimate  $C$  in Eq. A.6) we used an allometric relationship between tree height and crown area obtained from Metzger's (2002) data set on Serengeti acacias to generate a set of coefficients  $\mathbf{c}$ , with rounded values of 1, 3, 6, 9, 14, and 20 m<sup>2</sup> for size classes 1 through 6, respectively.

The Pellew tree population model does not take into account the effects of rainfall on tree growth (Pellew 1983), since the model was developed for a single site within the Serengeti ecosystem. The SD model, however, is designed to be applied over a much broader spatial scale, and given the marked rainfall gradient within the GSE, we considered it important to account for variation in tree growth across this gradient. We used a data set documenting tree radial

increments as a function of annual precipitation over 25 years from Mariaux (1975) to derive a linear relationship between growth and rainfall in *A. tortilis*. Assuming that the relationship between these two variables is similar in the Serengeti and West African Sahel, we used the slope of the regression conducted on Mariaux's (1975) data set to adjust our tree growth coefficients ( $g_{ij}$ ) as follows:

$$g'_{ij} = \frac{(aR_{ann} + b)}{d_0} g_{ij} \left(1 - \frac{n_6}{K_T}\right) \quad (\text{A.17})$$

where  $a$  and  $b$  are the slope and intercept of the rainfall-growth regression, respectively, and  $d_0$  is the mean radial increment of *A. tortilis* at Seronera.

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TABLE A1. State variables and parameters used in the SD model (parameters used in the sensitivity analysis are in bold font). Intermediate or derived variables (e.g.,  $t_{grow}$ ) are not listed.

Fitted parameters are denoted with an asterisk.

| Symbol       | Value  | Units                            | Description   |
|--------------|--------|----------------------------------|---|
| $G$          |        | $\text{g m}^{-1}$                | green grass   |
| $D$          |        | $\text{g m}^{-1}$                | dry grass   |
| $W$          |        | $\text{ha}^{-1}$                 | wildebeest  |
| $E$          |        | $\text{ha}^{-1}$                 | elephants   |
| $T_{1-6}$    |        |                                  | trees (six size classes)  |
| $R_{ann}$    |        | mm                               | annual rainfall   |
| $R_{day}$    |        | mm                               | daily rainfall  |
| $N$          |        | %                                | plant nitrogen  |
| $\psi^*$     | 0.0167 | $\text{mm}^{-1}$                 | rainfall effect on maximum grass growth                             |
| $\theta$     | 2.5    |                                  | neg. exponential parameter for tree-grass competition               |
| $\mu_0^*$    | 141    | $\text{g m}^{-1}$                | rainfall effect on grass carrying capacity (intercept)              |
| $\mu_1^*$    | 0.264  | $\text{g m}^{-1} \text{mm}^{-1}$ | rainfall effect on grass carrying capacity (slope)                  |
| $\rho$       | 0.5    |                                  | shading effect of D on production of G                              |
| $\sigma^*$   | 46     | $\text{g m}^{-1}$                | parameter to shift incremental growth curve of grass towards origin |
| $\delta_G$   | 0.061  | $\text{d}^{-1}$                  | decay rate for G  |
| $\delta_D^*$ | 0.0012 | $\text{d}^{-1}$                  | decay rate for D  |
| $f^*$        | 0.42   |                                  | fraction of decaying G moving into compartment D                    |
| $\tau$       | 0.01   | $\text{ha d}^{-1}$               | grass losses to trampling   |
| $g_0$        | 0.6    |                                  | maximum proportion in a cell occupied by grass                      |
| $\kappa_1^*$ | 0.061  | $\text{g}^{-1} \text{m}^2$       | slope for effect of biomass D on area burned                        |
| $\kappa_2^*$ | 3.7    |                                  | intercept for effect of biomass D on area burned                    |
| $s$          | 1.7    | $\text{y}^{-1}$                  | seedling recruitment rate   |
| $m$          | 0.01   | $\text{y}^{-1}$                  | adult tree natural mortality rate                                   |

|                                    |         |                                      |  |
|------------------------------------|---------|--------------------------------------|--|
| $g_{i,j}$                          |         |                                      | tree growth coefficients in matrix <b>G</b>  |
| $e_{i,j}$                          |         |                                      | elephant damage coefficients in matrices <b>E</b> <sup>1</sup> and <b>E</b> <sup>2</sup> |
| $f_{i,j}$                          |         |                                      | fire damage coefficients in matrices <b>F</b> <sup>1</sup> and <b>F</b> <sup>2</sup>     |
| <b>a</b>                           | 0.0071  | mm mm <sup>-1</sup>                  | rainfall effect on tree growth (slope)   |
| <b>b</b>                           | 0.61    | mm                                   | rainfall effect on tree growth (constant)  |
| <b>d</b> <sub>0</sub>              | 6.6     | mm                                   | tree annual diameter increase at mean rainfall   |
| $\alpha_W$                         | 1.05    | g ha m <sup>-2</sup> d <sup>-1</sup> | max wildebeest cropping rate   |
| $\beta_W$                          | 9.9     | g m <sup>-2</sup>                    | biomass at which wildebeest intake is 50% of max   |
| $dvi_G$                            | 0.54    | g ha m <sup>-2</sup> d <sup>-1</sup> | wildebeest max. daily voluntary intake of G  |
| $dvi_D$                            | 0.44    | g ha m <sup>-2</sup> d <sup>-1</sup> | wildebeest max. daily voluntary intake of D  |
| $\alpha_E$                         | 9.5     | g ha m <sup>-2</sup> d <sup>-1</sup> | max elephant grass cropping rate   |
| $\beta_E$                          | 172     | g m <sup>-2</sup>                    | biomass at which elephant grass intake is 50% of max                                     |
| <b>b</b> <sub>W</sub> <sup>*</sup> | 0.00049 | d <sup>-1</sup>                      | max per capita population growth for wildebeest  |
| <b>m</b> <sub>W</sub> <sup>*</sup> | 0.0032  | d <sup>-1</sup>                      | max mortality rate for wildebeest  |
| <b>a</b> <sub>W</sub> <sup>*</sup> | 0.21    | ha g <sup>-1</sup> m <sup>2</sup>    | effect of G on wildebeest mortality  |
| <b>q</b> <sup>*</sup>              | 3.15    |                                      | habitat preference parameter   |
| <b>φ</b>                           | 2.0     |                                      | emigration threshold parameter   |

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