Individual-based model of the Konik horse population

Model description

Nika Galic ngalic2@unl.edu

The model description follows the ODD protocol for describing individual- and agent-based models (Grimm et al. 2006, Grimm et al. 2010). The ODD is for the model version 5 ("Koniks_v5.nlogo".)

Purpose

The main purpose of the model is to explore how resource competition shapes individual life history and its feedback on dynamics of a horse population in a seasonal environment (De Roos et al. 2009). Specifically, the model investigates the link between prescribed growth in body size, population dynamics and density dependence through population feedback on available resources.

The model parameters are based on the Konik horse population is Oostvaardersplassen in The Netherlands. This model version is non-spatial.

Entities, state variables, and scales

Entities in the model are individual horses and the environment.
Individual state variables are age [days], structural mass [kg], fat mass [kg], gender/breed [foal, male, female], lifespan [days]. We also distinguish between gestating and lactating adult females. Pregnant females have the structural mass of the fetus [kg] as an additional state variable. Foals are horses up to 365 days of age.

The environmental state variable is the resource, i.e. vegetation [kg], which has seasonal dynamics.

Time is represented continuously, but the model implementation is based on discrete time steps – time steps can be modified by the user (time steps smaller than one day will result in more accurate, but much slower simulation). There are 365 days in a year. Simulations start on day 1 (April 1), corresponding roughly to the start of the vegetation season (in NW Europe), and go for 100 years or until there are no surviving individuals left. The output is evaluated only after 15 years to avoid transitional effects.

The table with all parameters and their distributions is provided at the end of this document (Table 1).
The Konik population model is programmed within the NetLogo platform (Wilensky 1999).

Process overview and scheduling

The dynamics of the following state variables are described by ordinary differential equations, which are implemented as difference equations (Euler method): structural mass growth, fat mass dynamics and resource dynamics. Reproduction (both probability to become pregnant and birthing) and mortality (background and starvation) are discrete events.

Every time step, the following processes are scheduled for all individuals in a randomized sequence for each process; state variables are updated at the end of the time step (asynchronous updating):

For each individual [

Aging (Increase age of individuals by designated time step)

If **Background mortality**

Delete from the population

Else - calculate changes in state variables

Resource intake

Structural mass growth

- **fetal growth in pregnant females**

Lactation – only lactating females

Fat mass dynamics – Energy gains – Energy losses

Starvation mortality – Mortality if under starvation threshold

]

Vegetation dynamics

For each individual [

Update state variables

]

Update vegetation

For females > 3 years [

Reproduction – fixed probability to become pregnant, birth of foals on 1st April

]

Update plots and output

Design Concepts

Basic principles. The model is based on basic rules for energy acquisition and allocation of energy to different metabolic processes in ungulate grazers in a seasonal environment (De Roos et al. 2009). The seasons are implemented as vegetation dynamics following seasonal growth representative of NW Europe.

Emergence. Individual level state variables emerge from dynamics of metabolic processes and indirect competition for resources, whereas population dynamics and characteristics emerge from individual level characteristics.

Sensing. The magnitude of resource acquisition, vegetation and milk production and consumption (for foals only), are regulated by the body condition of individuals, modeled as the fat-to-total-mass ratio. Individuals as assumed to "know" this condition. Those in good condition acquire half as much resources as starved individuals. Similarly, mares with foals in good condition produce less milk for them.

Interaction. Individuals interact indirectly with each other through competition for resources. Lactating mares and their foals have a direct link with each other manifested in the amount of milk produced dependent on the foal's fat-to-total-mass ratio. If the lactating female dies, its foal dies too.

Stochasticity. Mortality (background and starvation) and impregnation are stochastic events.

Observation. We observe structural mass and fat mass dynamics of individuals of various ages in the population, fat-to-total mass ratio, population age distribution, population abundance, resource and milk intake of foals and vegetation dynamics. All the model output is plotted in daily time steps.

Initialization

Simulations start on day 1 (April 1), corresponding roughly to the start of the vegetation season (in NW Europe). The initial population is set to 500 three year-olds, with a maximum fat-to-total mass ratio (0.3). Approximately half of the individuals are non-pregnant and non-lactating females. The amount of resource is set to 10^3 tons which is below the minimum carrying capacity of the system.

The following pseudo-code gives an overview of the initialization process

```
Initialize global parameters
Initialize resource
Initialize individuals [
        set gender
        set age
        set structural mass
        set fat mass
        set lifespan  ]
```

Input data

The model does not include external input for environmental variables, i.e. there are no external drivers of system behavior such as temperature, rainfall etc.

<u>Submodels</u>

The population model includes the following submodels: background mortality, resource intake, lactation, fat mass dynamics, starvation mortality, resource dynamics and reproduction. These are described in detail below.

BACKGROUND MORTALITY

Garrot and Taylor (1990) analyzed the survivorship of a feral horse population in Montana, USA and fitted a survivorship model based on individual age, *a*. Horses lived up to 24 years of age with a steady decrease in survival after 16 years of age.
The Konik horses tend to live up to 30 years (Anonymous 2004) and we therefore adjusted Garrot and Taylor's survivorship model to fit the Konik horse population (Figure 1)

$$S(a) = e^{[-\mu_b \cdot a - e^{-\alpha_m/\alpha_s} \cdot (e^{a/\alpha_s} - 1)]} \qquad \text{Eq. 1}$$

where μ_b is the background mortality parameter [d^{-1}], α_m is the horses' modal age of senescence [d], and α_s is the standard deviation in age of senescence [d].

In the model, at initialization and birth each individual is assigned a random value between 0 and 1 which fixes their lifespan. Individuals die when they reach the age at which the value of the

survivorship function is smaller than the randomly assigned number. Lactating females are directly linked to their foal's survival and if such a female dies, her foal dies with her.

This is covered in the *backgroundMortality* procedure that is run each day in the simulation.

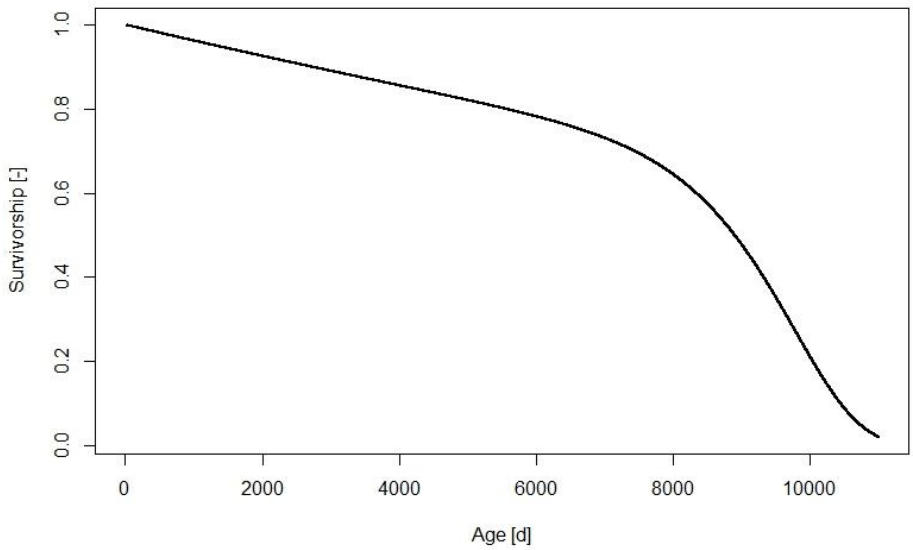

Figure 1. Survivorship of the Konik horse population, as a function of horses' age, *a,* [d].

RESOURCE INTAKE

As grazers, Konik horses prefer feeding on dry grasslands, but also reed and dead herbs are grazed when the grasses are scarce (Vulink 2001).
The intake rate *I (V, S, F, W)* scales allometrically with structural mass *S,* the amount of fat reserves *F,* total mass *W* and the amount of available resource *V*

$$I(V,S,F,W) = \alpha \cdot S^{3/4} \cdot \frac{V}{\beta + V} \cdot \frac{1}{1+e^{-\eta\cdot(\rho\cdot W - F)}} \qquad \text{Eq. 2}$$

Where α is the maximum intake rate [kg $kg^{-3/4}$ d^{-1}], and β is the half saturation constant [kg], i.e. the amount of vegetation at which the herbivores intake rate is half of the maximum size.
We assumed that an individual horse only realizes its maximum intake rate if it's fat-to-total mass is well below its maximum and that it feeds only half as much when its fat-to-total mass ratio is at its maximum. This process of satiation is governed by the last term in eq. 2. The more fat mass an individual has, the less its intake will be and vice versa.
The η in the last term is a scaling constant [kg^{-1}] that controls the steepness of the intake rate.
Pregnant females add the mass of their fetus to their total mass, *W*. The amount of resource consumed in a given time step is immediately subtracted from the total amount of available resource.
This process is covered in the *resourceIntake* procedure in the model.

STRUCTURAL MASS GROWTH

The total wet body mass W [kg] of an individual horse consists of structural mass *S* [kg] and fat mass *F* [kg] the latter amounts to a maximum of 30% of the total body mass (Illius and O'Connor 2000), denoted as ρ [-].

$$W = S + F \text{ where } F_{\max} = \rho \cdot W$$

The mares (3 years and older) are impregnated on ca. 1 May (day 30) with a fixed probability β (Anonymous 2004). Mares can lactate and be pregnant at the same time.

The embryo starts to develop after a 57-day delay period τ_D [d] (Kooijman 2000).Gestation in equids is long, ranging from 330 to 390 days and we set the duration to a total of 335 days (Tischner and Klimczak 1989).

Kooijman (2000) describes the structural growth of a fetus as

$$Sf(\tau_R) = (\frac{1}{3}\nu \cdot (\tau_R - \tau_D))^3 \qquad \text{for} \quad \tau_R > \tau_D \qquad \text{Eq. 3}$$

with *v* as a conductance rate [cm d^{-1}] for fetal structural body mass growth and τ_R the time [d] since start of pregnancy, i.e. the age of the fetus (Figure 2).

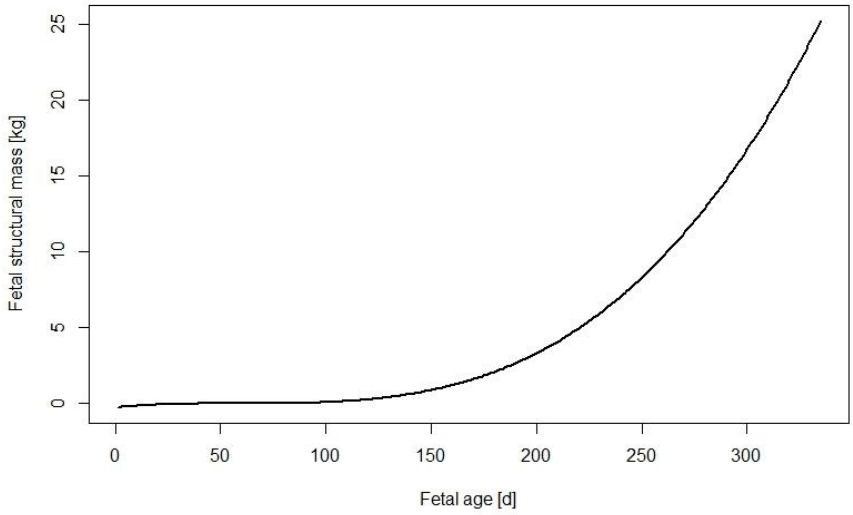

Figure 2. Structural mass growth [kg] of a horse fetus as a function of age [d].

Fetal mass is added to the total body mass of its mother. At the end of the gestation period, the foals are born on 1 April the following year and form a direct link with their mother. We assumed the same fat-to-total mass ratio for the foal at birth as its mother. The foal's fat reserves are subtracted from its mother's. Foals are born with a fixed structural mass (Tischner 1985, Tischner and Klimczak 1989).

After birth, individuals grow according to the von Bertalanffy growth (Kooijman 2000)

$$S(a) = (S^{1/3}{}_{\max} - (S^{1/3}{}_{\max} - S^{1/3}{}_{b}) \cdot e^{-\gamma \cdot a})^3 \qquad \text{Eq. 4}$$

with an individual growth rate γ [d^{-1}], maximum attainable structural mass S_{max} [kg] and structural mass at birth S_b [kg] (Figure 3).

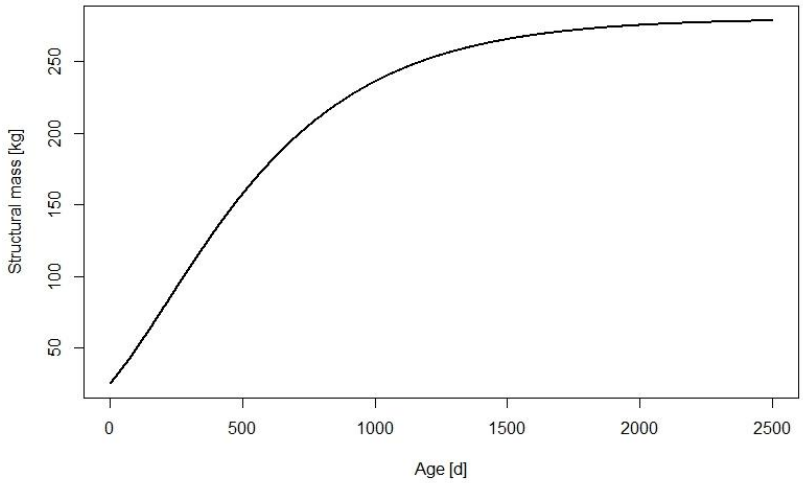

Figure 3. Horse structural mass growth [kg] as a function of age [d].

Structural mass growth (fetal and non-fetal) is covered in *structuralGrowth* procedure in the model.

LACTATION

After giving birth, mares form a link with their foals and start producing milk for them. The lactating period is set to 12 full months of a foal's age. If the mare has another foal after these 12 months, she continues to lactate, if not, the lactation is stopped.

Foal's milk intake depends on the amount of its current fat reserves that as modeled by the last term in eq. 5. When the foal has maximum fat mass (F=0.3W), its milk intake is halved. The same goes for the lactating mare; the production of milk decreases as the foal acquired more fat mass. The amount of daily milk production

$$L(a_f, W, F_f, W_f) = \lambda_m \cdot W \cdot \frac{e^{-\lambda_s \cdot a_f}}{1 + e^{-\eta \cdot (\rho \cdot W_f - F_f)}} \qquad \text{Eq. 5}$$

depends on the maximum daily production rate λ_m [d^{-1}] and declines with the rate λ_s [d^{-1}] as the foal gets older, a_f . According to Vulink (2001), the production declines to less than 1% of mare's total mass in the last period of lactation.

Foals have access to both milk and vegetation from their birth on, but the dynamics of milk production and the total mass of the foal determining the vegetation intake ensure that in the first months of their life, foals obtain more energy from mares' milk.
The milk production is stopped when either the mother or the foal dies or when the foal reaches one year of age.

This process is covered in the *lactation* procedure in the model.

FAT RESERVE DYNAMICS

Energy allocation

Energy is acquired through the processes of milk intake (foals only, described in **LACTATION**) and through vegetation intake (described in **RESOURCE INTAKE**).

Energetic requirements for metabolic maintenance include the amount of digestible energy for zero-body-mass-change plus normal activity of a non-working horse. The basal metabolic rate *BMR* [MJ d^{-1}] is a function of body mass $W^{3/4}$ (Kleiber 1947, Reiss 1989)

$$BMR = 70 \cdot W^{3/4} \qquad \text{Eq. 6}$$

Allowing for some basic daily activities, the metabolic maintenance costs C_M [MJ d^{-1}] amount to

$$C_M = 2 \cdot BMR$$
$$C_M(W) = \sigma_M \cdot W^{0.75} \qquad \text{Eq. 7}$$

where σ_M is the metabolic cost constant [MJ $kg^{-3/4}$ d^{-1}] (Kleiber 1947, Reiss 1989, Flachowsky and Kirchgessner 1998).

Daily energetic costs for structural tissue growth are proportional to the rate of change in structural mass (eq. 4), and increase with horses' age (Anonymous 1989), following

$$C_G(a,S) = \sigma_G \cdot e^{k \cdot a} \cdot \frac{dS}{da} \qquad \text{Eq. 8}$$

with σ_G as the initial cost of structural tissue growth [MJ kg^{-1}], and k as the rate of change in the energetic costs of growth [d^{-1}] which increases with an individual's age a. As the horses get older, daily increments in structural mass growth steadily become smaller resulting in very small growth costs in older individuals.

Energetic costs for fetal development are paid by pregnant females and are proportional to the rate of change in fetal structural mass (eq. 3), with a fixed proportionality constant σ_G.

The estimated energy requirement per kg milk production σ_L [MJ kg^{-1}] (Anonymous 1989, Vulink 2001) is paid by the lactating female (eq. 5), and the yield for an individual foal is converted to energy with a constant ε_M [MJ kg^{-1}] (Mariani et al. 2001).

To sum up, the following energy acquisition and allocation processes contribute to the fat reserve dynamics:

1) I_R - Intake of Resource
2) I_M - Intake of Milk – foals only
3) C_M - Costs of metabolic Maintenance
4) C_G - Costs of structural Growth
5) C_P - Costs of fetal growth
6) C_L - Costs of Lactation

Dynamics of fat reserves of an individual equals the balance of listed energy acquisition and allocation processes (Figure 4):

1) Foal fat reserve dynamics

$$\frac{dF_f}{dt} = \left[\underbrace{\pi(\tau_S) \cdot I(V,S,F,W)}_{I_R} + \underbrace{\varepsilon_m \cdot L(\tau_L, W, F_f, W_f)}_{I_M} - C_M(W) - C_G(a,S) \right] \cdot \varepsilon^{-1} \quad \text{Eq. 9}$$

2) Female fat reserve dynamics (one or two terms can be omitted depending on the status (pregnant and/or lactating) of the female)

$$\frac{dF_{fm}}{dt} = \left[\underbrace{\pi(\tau_S) \cdot I(V,S,F,W)}_{I_R} - C_M(W) - C_G(a,S) - \underbrace{\sigma_G \cdot \left(\frac{1}{9} \cdot v^3 \cdot (\tau_R - \tau_D) \right)^2}_{C_P} - \underbrace{\sigma_L \cdot L(\tau_L, W, F_f, W_f)}_{C_L} \right] \cdot \varepsilon^{-1}$$

Eq. 10

3) Male (and non-pregnant and non-lactating females) fat reserve dynamics

$$\frac{dF_m}{dt} = \left[\underbrace{\pi(\tau_S) \cdot I(V,S,F,W)}_{I_R} - C_M(W) - C_G(a,S) \right] \cdot \varepsilon^{-1} \quad \text{Eq. 11}$$

Fat reserve dynamics may be anabolic ($\frac{dF}{dt} > 0$), in which case there is a surplus of energy which is then stored in fat tissue. Alternatively, reserves may be used to cover the energy requirements under conditions of resource scarcity, in which case reserve dynamics are catabolic ($\frac{dF}{dt} < 0$). The parameter ε determines the conversion efficiency from reserves into energy [MJ kg^{-1}], which is assumed different for anabolic ($\varepsilon = \varepsilon_a$; Table 1) and catabolic reserves dynamics ($\varepsilon = \varepsilon_c$; Table 1; (Baxter 1989, Illius and O'Connor 2000))

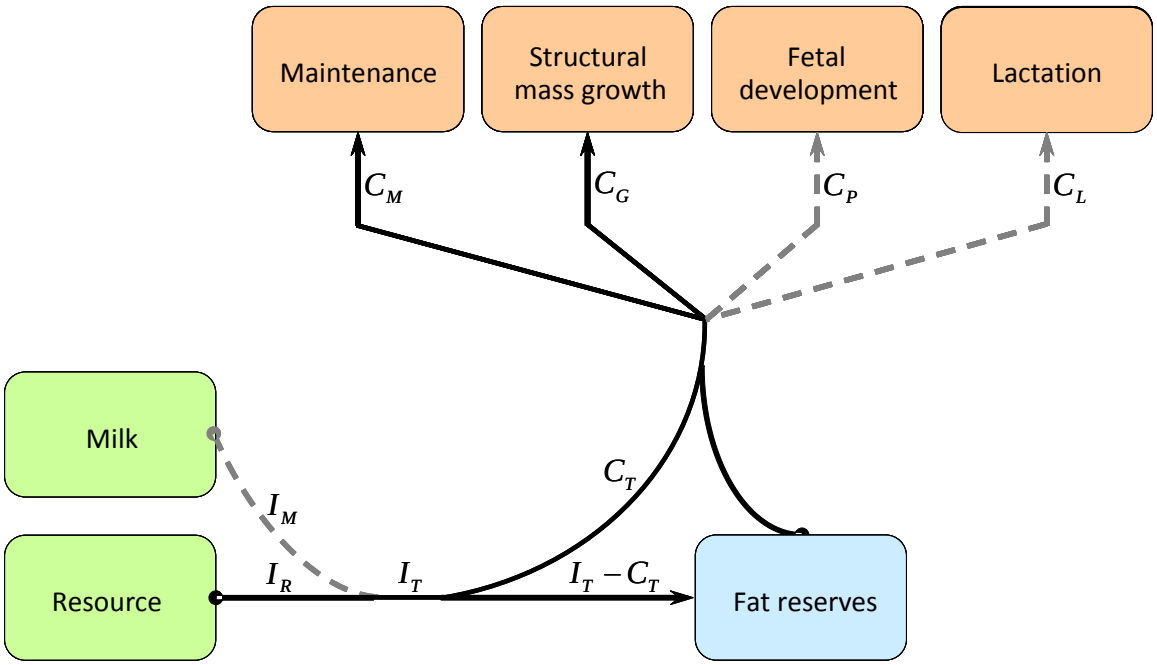

Figure 4. Schematic overview of the individual energy budget. Energy acquisition processes are characterized by different intake rates *I*, while flows of energy allocation are characterized by different rates *C*. Solid black lines represent energy flows that occur in all type of individuals independent of their age and sex. Energy flows occurring only in foals (I_M), pregnant (C_P) or lactating females (C_L) are indicated with grey dashed lines.

The fat reserve dynamics are modeled with the *reserveDynamics* procedure.

STARVATION MORTALITY

Large ungulates are known to die of starvation when the environmental conditions are rough (Cederlund et al. 1991) and/or due to density-dependent causes (Clutton-Brock et al. 1997, Coulson et al. 2000, Clutton–Brock and Coulson 2002). Relatively high periodic mortality, typically at the end of the winter, has been observed repeatedly in large ungulate populations in the Oostvaardersplassen (Anonymous 2004).

In the model, we assume that once the fat-to-total mass ration falls under a specified threshold, individuals' probability of starvation mortality is increased

$$S(F,W) = e^{-\mu_S \cdot (\rho_S \cdot \frac{W}{F} - 1)} \qquad \text{for } F/W < \rho_S \qquad \text{Eq. 12}$$

With a starvation mortality rate μ_S, that scales the severity of the starvation mortality [d^{-1}]. Once their fat-to-total mass ratio fall below 0.1 (i.e. 10% of fat reserves left), denoted the parameter ρ_S [-], the individual has an increasing probability of dying due to starvation.

If a lactating female dies of starvation, it is assumed the foal dies too.
Starvation mortality is modeled with the *starvationMortality* procedure.

RESOURCE DYNAMICS

The vegetation dynamics is assumed to follow the seasonal environment of NW Europe, where the onset of the growing season starts in early spring (Vulink 2001). As the model is inspired by the Oostvaardersplassen system in the Netherlands, we roughly modeled the dynamics of dry grasslands. The most common species growing on dry grasslands are: *Cirsium arvense*, *Urtica dioica*, *Poa trivialis*, *Lolium perenne* and *Festuca rubra*. In the model, different species are aggregated into accessible resource for horses.

In the model, the resource follows semi-chemostat dynamics, with a re-growth rate r [d^{-1}] and maximum resource density K [kg] in absence of herbivores (eq. 14), as a function of the day in the season τ_S [d]

$$\frac{dV}{d\tau_S} = r \cdot (K(\tau_S) - V) - \sum_i I(V, S_i, F_i, W_i) \qquad \text{Eq. 13}$$

The second term describes the amount of resource consumed by the horses, as a function of the resource density V, structural S, fat F and total mass W of the horses (described in **RESOURCE INTAKE**). The total grazing equals the sum of amount grazed by each horse, indexed by i.

Seasonality in resource growth was implemented a sinusoidal function for the maximum resource density of the system K (Turchin and Hanski 1997, Van De Wolfshaar et al. 2006) (Eq. 4)

$$K(\tau_S) = \begin{cases} V_{\max} + \frac{V_{\max} - V_{\min}}{2} \cdot (1 + (\sin \frac{180 \cdot \tau_S}{Z})^{\Theta}) & 0 \le \tau_S \le Z \\ V_{\max} + \frac{V_{\max} - V_{\min}}{2} \cdot (1 - (\sin \frac{180 \cdot (\tau_S - Z)}{(Y - Z)})^{\Theta}) & Z \le \tau_S < Y \end{cases} \qquad \text{Eq. 14}$$

with a maximum V_{max} [kg] and a minimum V_{min} [kg] resource density within a season, and the time since the start of the growing season τ_S [d] (Figure 5). Z represents the duration of the summer period and is set to 150 days and Y is a 365-day year. The shape of the sinusoidal function can be manipulated with Θ. If Θ is one, the shape of the vegetation growth is a pure sine function.

The mean digestible energy content of the vegetation decreases during the season and we model it with an empirically established relationship (Vulink 2001)

$$\pi(\tau_S) = \chi_m \cdot \sqrt{1 - \chi_S \cdot \tau_S^{\,2}} \qquad \text{Eq. 15}$$

where χ_m [MJ kg^{-1}]and χ_S [d^{-2}] are conversion constants. The assimilation efficiency of ingested resource hence depends on the time since the start of the season, τ_S.

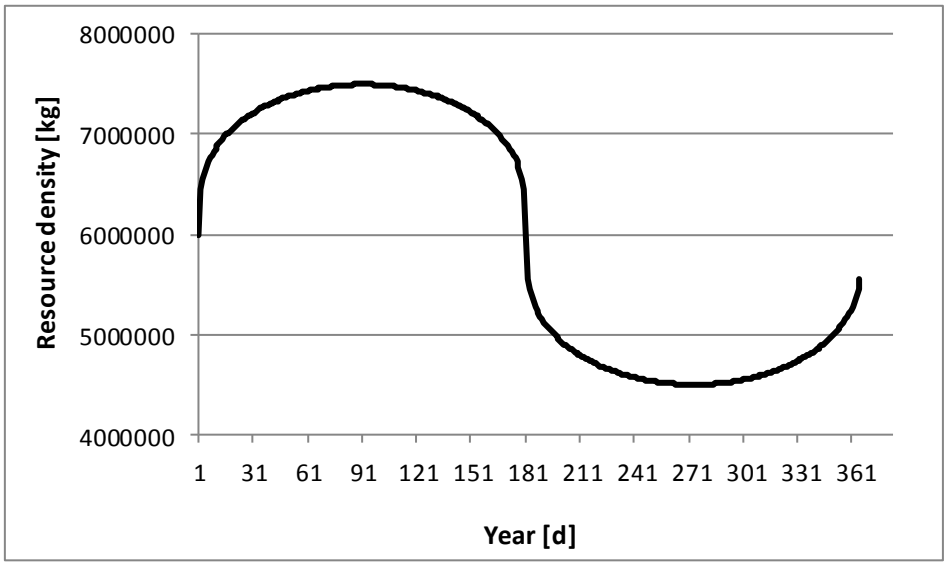

Figure 5. Maximum and minimum resource density [kg] in the whole system, in absence of grazers.

Vegetation dynamics is modeled with the *vegetation* procedure.

REPRODUCTION

Large ungulates give birth in spring, typically between March and June (depending on the species) to one or two offspring (Tischner and Klimczak 1989, Clutton–Brock and Coulson 2002, Anonymous 2004).

We assumed a single offspring is born to a female after 335 days of gestation (Tischner and Klimczak 1989). Foals are of undetermined gender and their fat-to-total mass ratio equals those of their mothers, as we assumed maternal effects (Walton and Hammond 1938, Tischner and Klimczak 1989). The amount of fat mass transferred to foals is deducted from their mothers; all foals are born with a fixed structural mass (Tischner and Klimczak 1989).
Mothers are directly linked to their foals and when a female dies (due to starvation or background mortality), we assume the foal cannot survive on its own and dies too. Once the foals turn one year, this link is deleted; foals become independent yearlings and are assigned a gender (1:1 ratio).

For simplicity, we assume that all foals are born on the same day (April 1st). Also, females older than 3 years have a fixed probability (Anonymous 2004) of being impregnated on the same day, 30 days after foaling (ca. May 1st in the modeled year). Females can be pregnant and lactating at the same time.

Reproduction is modeled with the *reproduction* procedure.

Table 1: Model parameters. Sources: 1, Tischner and Klimczak (1989); 2, Vulink (2001); 3, Illius and O'Connor (2000); 4, Anonymous (2004); 5, Kooijman (2000); 6, Owen-Smith (2002); 7, calibrated; 8, Kleiber (1947), Reiss (1989), Flachowsky and Kirchgessner (1998); 9, Anonymous (1989); 10, Mariani et al. (2001); 11, Baxter (1989); 12, Garrot and Taylor (1990); 13, Turchin and Hanski (1997).

Parameter	Unit	Value	Description	Ref.
S_b	kg	25.5	Structural mass at birth	1
$S_{\max}$	kg	280	Maximum structural mass	2
γ	d^{-1}	0.0023	Growth rate in structural mass	1
ρ	-	0.3	Target reserves mass as fraction of *W*	3
o	-	0.56	Fraction of females becoming pregnant	4
τ_D	d	57	Delay in start of fetal development	4,5
ν	$cm \cdot d^{-1}$	0.32	Conductance constant	5
α	$kg \cdot kg^{-3/4} \cdot d^{-1}$	0.156	Scalar constant in maximum grazing rate	2
β	$kg \cdot ha^{-1}$	100	Half saturation constant in grazing rate	6
η	kg^{-1}	15	Steepness in satiation scaling of intake rate	7
σ_M	$MJ \cdot kg^{-3/4} \cdot d^{-1}$	0.6	Scalar constant in metabolic costs	8
σ_G	$MJ \cdot kg^{-1}$	40	Initial/fetal cost of structural mass growth	9
σ_L	$MJ \cdot kg^{-1}$	3.31	Cost of milk production	2,9
κ	d^{-1}	0.0015	Rate of increase in growth costs	9
λ_m	d^{-1}	0.03	Maximum milk production as fraction of *W*	2
λ_s	d^{-1}	0.004	Rate of decline in milk production	2
ε_m	$MJ \cdot kg^{-1}$	1.9	Milk energy content	10
ε_a	$MJ \cdot kg^{-1}$	54.6	Anabolic reserves conversion efficiency	3,11
ε_c	$MJ \cdot kg^{-1}$	39.3	Catabolic reserves conversion efficiency	3,11
μ_b	d^{-1}	$3.86 \cdot 10^{-5}$	Background daily mortality	4
α_m	d	9855	Modal age of senescence	12
α_s	d	912.5	Standard deviation in age of senescence	12
μ_s	d^{-1}	0.012	Scalar constant in starvation mortality	7
ρ_s	-	0.1	Reserves-mass ratio where starvation starts	7
r	d^{-1}	0.002	Resource regrowth rate	2
$V_{\max}$	$kg \cdot ha^{-1}$	$6000 \cdot A$	Maximum summer resource density	2
$V_{\min}$	$kg \cdot ha^{-1}$	$2000 \cdot A$	Minimum winter resource density	2
Θ	-	0.3	Steepness in seasonality shift	13
χ_m	$MJ \cdot kg^{-1}$	10.7	Resource energy content at start of summer	2
χ_s	d^{-2}	$3.5 \cdot 10^{-6}$	Rate of decline in resource energy content	2
A	ha	750	Total habitat area	4
Z	d	150	Summer duration	7
Y	d	365	Year length	7

Model variant – extreme weather

To test the effects of extreme weather conditions, in the form of snow cover, on individual bioenergetics and population dynamics, we implemented a probability that snow cover will occur in a given year and the length of the snow cover period. Both are defined by the model user on GUI (snowProbability and snowCoverLength).

During the snow cover period, there is no resource growth or resource intake by all grazing individuals in the population. All the baseline model processes are exactly the same as previously described.

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