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How resource competition shapes individual life history for nonplastic growth: ungulates in seasonal food environments

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Abstract. We analyze an age-, size- and sex-structured model to investigate how the interplay between individual-level energy budget dynamics and the feedback of population grazing on resources shapes the individual life history and the dynamics of ungulate populations, living in a predator-free, seasonal resource environment. We formulate a dynamic energy budget model for individual energetics, which accounts for energy requirements for maintenance and growth, and possibly pregnancy and lactation. Growth in structural mass is assumed prescribed. Dynamics of energy reserves are the resultant of energy acquisition through grazing and suckling of milk and the aforementioned energy-consuming processes. The dynamic energy budget model is used as the core for an individual-based population model, which captures general features of ungulate life history and population dynamics, although it is parameterized for a particular system.

Model predictions reveal a characteristic dynamic pattern, in which years with low death tolls (<10% of the population dying) alternate with a single year of high death toll (up to 40% of the population dies). In these “collapse” years almost all individuals younger than 2 years die, creating holes in the population age distribution. The die-off of these age classes is shown to be caused by the energy requirements for growth that these individuals face. Individuals between 1 and 2 years of age are more at risk than foals, because they are burdened with the legacy of a poor body condition developed throughout their first winter. The characteristic dynamic pattern is more pronounced at high levels of resource productivity. In contrast, neither a period of snow cover, during which all foraging stops, nor a dependence of fecundity on female body condition change dynamics significantly.

Key words: dynamic energy budget model; life history; population collapses; population dynamics; structured population models; ungulates.

INTRODUCTION

Dynamics of ungulate populations are shaped by a combination of density-dependent and environmental factors (Gaillard et al. 2000). Density dependence tends to kick in primarily when populations approach or overshoot a threshold density with only weak regulation at low densities (Fowler 1987, Sinclair 2003). As a consequence, ungulate populations can overexploit their food resources and fluctuate wildly (Clutton-Brock et al. 1997, Sæther 1997, Côté et al. 2004). These population fluctuations are, however, exacerbated through interplay with environmental fluctuations, in particular seasonal and year-to-year fluctuations in resource availability (Vucetich and Peterson 2004) and climate (Coulson et al. 2000, Forchhammer et al. 2001). Increasing population densities have been correlated with changes in various life history traits (reviewed by, among others, Fowler 1987, Sæther 1997, and Gaillard et al. 2000). In particular, at high population densities growth in body

mass is reduced (Skogland 1983, Bonenfant et al. 2002, Weladji and Holand 2003), reproduction is delayed (Skogland 1986, Festa-Bianchet et al. 1995), and fecundity of prime-aged females is lower (Clutton-Brock et al. 1987, Albon et al. 2000, Coulson et al. 2000). Furthermore, high densities also decrease survival of individuals in their first year of life (Clutton-Brock et al. 1991, Albon et al. 2000, Coulson et al. 2001, Forchhammer et al. 2001), of yearlings (Clutton-Brock et al. 1987, Forchhammer et al. 2001), as well as of adults (Albon et al. 2000, Forchhammer et al. 2001, Bonenfant et al. 2002), mainly during the winter period.

Body size and growth therein play a central role in these density-dependent effects. Body size is an important determinant of first-year survival and age at first reproduction (Gaillard et al. 1996, Loison et al. 1999), while growth conditions during early development may affect life history processes later in life (Lindström 1999). Growth in body size is related to the quantity of food available as well as to its quality (Crawley et al. 2004). Environmental conditions that increase food quantity and quality, such as low snow depths during winter (Cederlund et al. 1991, Loison et al. 1999), long

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photosynthetic period during summer (Ericsson et al. 2002, Herfindal et al. 2006) and cold, wet summer weather (Gaillard et al. 1996), are associated with large body masses, while body mass is negatively affected by competition for food (Skogland 1983, Gaillard et al. 1996, Forchhammer et al. 2001, Weladji and Holand 2003). As a consequence, body size and growth are important determinants of population dynamics, especially through their effects on juvenile survival and the age at first reproduction (Gaillard et al. 1998, 2000).

These studies on ungulate dynamics reveal that individual life history and population dynamics are intricately intertwined. On the one hand individual life history, in terms of, for example, juvenile survival and onset of reproduction, determines the resulting population dynamics. On the other hand the type of life history that can be realized depends on the availability of food and hence indirectly on population dynamic feedback on this availability. In other words, life history shapes population dynamics, which in turn shapes individual life history through density dependence. This complex interrelationship between life history and population dynamics includes three main components: (1) the dependence of life history development (e.g., growth, survival, maturation) on resource availability, (2) the ability of individuals in different stages of their life history to compete for resources, and (3) the feedback of population grazing on resource availability. We argue that empirical and experimental studies alone cannot fully unravel the interrelationship, as they cannot completely disentangle these main components. To fully understand the interrelationship between life history and population dynamics we therefore see a need for population dynamic modeling that explicitly and mechanistically accounts for individual life history and more specifically for the three main components that link the two.

Such modeling studies of the interrelationship between individual life history and population dynamics have been carried out for waterfleas (McCauley et al. 1996, De Roos et al. 1997) and fish (Persson et al. 1998, Claessen et al. 2000, De Roos et al. 2003) using (physiologically) structured population models (Metz and Diekmann 1986, De Roos 1997). Structured population models are based on a core model of the individual energy budget dynamics, which describes food intake and its subsequent use for growth, maintenance, and reproduction as a function of food availability and the physiological traits (age, size, energy reserves) of an individual. A variety of dynamic energy budget (DEB) models exist, ranging from more species-specific (Kooijman and Metz 1984, Gurney et al. 1990, Persson et al. 1998) to more generic (Kooijman 2000, Lika and Nisbet 2000), which, however, all assume that food acquisition is the limiting process in the energy budget. Food availability therefore fully determines the realized growth trajectory and the asymptotic body size. This food-dependent plasticity of growth in body size has been identified as the most important determinant of

population and community dynamics that result from these types of DEB models (De Roos and Persson 2005, Persson and De Roos 2007). Food-dependent growth gives rise to distinct types of population cycles that are either dominated by young, juvenile individuals or by adults (Persson et al. 1998, De Roos and Persson 2003).

In contrast, little is known about the interrelationship between individual life history and population dynamics for the case when growth trajectories and asymptotic size are mostly under genetic control and only influenced to a minor extent by environmental (food) conditions (but see Illius and Gordon 1999, Illius and O'Connor 2000). We will refer to such a growth pattern as "prescribed" growth (also referred to as "constrained" growth; Sebens 1987). Prescribed growth is exemplified by most aquatic and terrestrial vertebrates, including ungulates.

To investigate the link between prescribed growth in body size, population dynamics, and density dependence through population feedback on available resources we formulate a dynamic energy budget model that captures the main energetic processes in the life history of an individual ungulate. We analyze the consequences of this dynamic energy budget model for individual life history and population dynamics under conditions of seasonal variation in resource availability. The model captures the general features of ungulate life history, in particular foraging, maintenance, growth, and reserves dynamics. In addition, it distinguishes between 0 and 1-year-olds, yearlings, adult males and adult females. For adult females the energetic costs associated with pregnancy and lactation are explicitly accounted for. Despite its generic nature the model is parameterized for a particular system, the Konik horse population in the enclosed nature reserve Oostvaardersplassen in the Netherlands (Vulink 2001, Anonymous 2004). Konik horses have been introduced to this nature reserve in addition to Heck cattle and red deer for management purposes and live there in complete absence of predators. We choose this particular population living under these rather artificial conditions primarily because it has recently been the subject of a heated public debate about the necessity for supplementary feeding during severe winter conditions when snow cover limits the grazing for resources (ICMO 2006).

We want to emphasize that our aim is not simply limited to investigating plausible explanations for observed population dynamics patterns, such as regular fluctuations in ungulate abundance. Such an aim might not require the use of individual-based population models, but could be investigated using more aggregated, unstructured models instead (Owen-Smith 2002). Nor do we restrict our focus to investigating density-dependent effects on individual life history, which can be addressed using time series analysis of observed population dynamics (Coulson et al. 2004). Rather, we aim for unraveling the mutual dependence of, and the interplay between, population dynamics and density-dependent life history of ungulates. We therefore focus

our analysis on the relation between the buildup of energy reserves by individuals of different ages and sizes dependent on food availability and population density, its consequences for survival during the subsequent winter, and ultimately, the effects on population dynamics.

MODEL FORMULATION AND PARAMETERIZATION

We formulate an individual-based model for an ungulate population, in which individuals are distinguished from one another by age, sex, size, energy reserves, and in the case of females, whether they are pregnant or lactating. Although general in design and structure, we have mostly parameterized the model on the basis of data for a particular population, the Konik horses in the nature reserve Oostvaardersplassen in the Netherlands, which has been studied extensively for conservation and management purposes (Vulink 2001, Anonymous 2004). The ungulates are assumed to live in a closed habitat area where they are not exposed to predation. They interact with their environment and with each other only through resource grazing. The resource exhibits temporal variability in productivity during the year, while spatial heterogeneity in resource productivity is neglected. The latter assumption is justified, as we focus on a horse population, and horses, as hindgut fermenters, have a wide array of forage species at their disposal, ranging from high-quality grasses to low-quality, high-fiber reed species. The year is subdivided into a summer and winter period of 150 and 215 days, respectively, with different resource productivities. Without loss of generality we chose 1 April to be day 1 of the year, which roughly corresponds to the start of the season with high productivity of the vegetation (Vulink 2001). Birth and death of ungulates are modeled as discrete events in time, while all other processes, including foraging, growth, reserves dynamics, and resource regrowth, progress in continuous time. We only account for individual-level dynamics in size and reserves, and do not take specific mineral and protein requirements into account. Furthermore, we do not account for a direct impact of temperature on individual energy budget dynamics, as temperature extremes rarely occur in the particular nature reserve we focus on. All functions describing the individual life history dynamics are summarized in Table 1. All model parameters are listed in Table 2, with their interpretation, default value, and the literature sources used for their estimation. By default we started simulations of population dynamics always with an initial population of 20 individuals introduced into a previously unexploited habitat. In the following we briefly discuss the important parts of the model.

Energy budget dynamics

Every individual is characterized by its individual state or *i*-state (Metz and Diekmann 1986, De Roos 1997), which in our case consists of six variables: age,

sex, structural mass (i.e., muscles, bones), reserves (mainly in the form of adipose tissue), pregnancy status, and lactation status. Total body mass W is the sum of both structural mass S and reserves F . For pregnant female individuals total mass also includes the structural mass of their developing fetus (Table 1: Eq. 5). As an idealization of a growth pattern that is mostly under genetic control and only to a limited extent influenced by environmental conditions, we assume individuals to exhibit prescribed, food-independent growth in structural mass. Following Kooijman (2000) we assume that fetal growth in structural mass follows a cubed power of the time since fetal development started, ending with the size at birth S_b at the end of the fetal development period T_p (Table 1: Eq. 3). After birth individuals follow a von Bertalanffy growth curve with an ultimate size S_m (Table 1: Eq. 4). We furthermore assume that there is a target ratio of reserves to total body mass $F:W$ referred to with the parameter ρ (Illius and O'Connor 2000).

Fig. 1 shows a schematic overview of the individual energy budget with the main processes of energy acquisition and use. Energy acquisition occurs through resource grazing and milk suckling, while energy is spent on maintenance and growth in structural mass, and possibly on energetic costs for fetal development and milk production. Our assumption of food-independent growth sets the model developed here apart from earlier energy budget models (Kooijman and Metz 1984, Gurney et al. 1990, Persson et al. 1998, Kooijman 2000, Lika and Nisbet 2000). The latter all assume growth to be food dependent and to occur only if food availability is sufficient. Because of the prescribed growth in our model all energy-requiring processes are functions of the individual state only and independent of resource density. Where earlier models can hence appropriately be viewed as “supply models,” our energy budget model describes a “demand system,” as sufficient energy has to be taken up to cover the energy demands, including those for growth.

All individuals forage on the resource following a grazing rate $G(V, S, F, W)$, which is a function of the resource (vegetation) density V , the structural mass S of the individual, and its reserves F (Table 1: Eq. 8). Maximum ingestion rate follows a three-quarters power scaling law with structural mass (Illius and O'Connor 2000, Vulink 2001, Brown et al. 2004) and a Holling type II functional response as a function of resource density (Illius and O'Connor 2000, Owen-Smith 2002). In addition, ingestion is a sigmoid function of the reserves:total mass ratio $F:W$, which limits resource ingestion when this ratio approaches or exceeds its target value ρ . The mean digestible energy content of the resource generally decreases during a growing season, which we model with an empirically established relationship (Table 1: Eq. 6; Vulink 2001). The assimilation efficiency of ingested resource (Table 1: Eq. 6) hence depends on the time t_s (Table 1: Eq. 1) elapsed since the start of summer.

TABLE 1. Model variables and equations.

Variable	Units	Symbols and equations	Equation no.
Model variables			
Resource density	kg/ha	V	
Age	d	A	
Reserves	kg	F	
Time since summer start	d	$t_s = t \bmod Y$	(1)
Time since start fetal development	d	$t_p = (t - \Delta_p) \bmod Y$	(2)
Structural mass (fetus)	kg	$S_p(t_p) = S_b(t_p/T_p)^3$ for $t_p < T_p$	(3)
Structural mass (horse)	kg	$S(a) = [S_m^{1/3} - (S_m^{1/3} - S_b^{1/3})e^{-\gamma a}]^3$	(4)
Total mass	kg	$W = \begin{cases} S + F + S_p(t_p) & \text{for pregnant females} \\ S + F & \text{otherwise} \end{cases}$	(5)
Resource environment			
Resource energy content		$E_R(t_s) = \chi_m \sqrt{1 - \chi_s t_s^2}$	(6)
Maximum resource density		$K(t_s) = \begin{cases} V_{\max} + \frac{V_{\max} - V_{\min}}{2} \left[1 + \left(\sin \frac{\pi t_s}{Z} \right)^\Theta \right] & 0 \leq t_s < Z \\ V_{\max} + \frac{V_{\max} - V_{\min}}{2} \left\{ 1 - \left[\sin \frac{\pi(t_s - Z)}{(Y - Z)} \right]^\Theta \right\} & Z \leq t_s < Y \end{cases}$	(7)
Resource grazing		$G(V, S, F, W) = \phi_c S^{3/4} \frac{V}{\phi_h + V} \frac{1}{1 + e^{-\eta(\rho W - F)}}$	(8)
Energy budget processes			
Resource assimilation		$I_R(t_s, V, S, F, W) = E_R(t_s)G(V, S, F, W)$	(9)
Milk suckling		$I_M(a, W_m, F, W) = \varepsilon_m \lambda_m W_m \frac{e^{-\lambda_s a}}{1 + e^{-\eta(\rho W - F)}}$ for $a < Y$	(10)
Metabolic costs		$C_M(W) = \sigma_M W^{3/4}$	(11)
Growth costs		$C_G(a, S) = 3\sigma_G e^{\kappa a} \gamma (S_m^{1/3} S^{2/3} - S)$	(12)
Pregnancy costs		$C_P(t_p) = 3\sigma_G S_b^2 / T_p^3$ for $t_p < T_p$	(13)
Lactation costs		$C_L(a_f, W, F_f, W_f) = \sigma_L \lambda_m W \frac{e^{-\lambda_s a_f}}{1 + e^{-\eta(\rho W_f - F_f)}}$ for $a_f < T$	(14)
Mortality			
Background survival function		$H_b(a) = \exp[-\mu_b a - e^{-\alpha_m/\alpha_s} (e^{a/\alpha_s} - 1)]$	(15)
Starvation probability		$H_s(F, W) = e^{-\mu_s(\rho_s W/F - 1)}$ for $F/W < \rho_s$	(16)

Notes: Model variables with subscript m and f refer to the values of a mother and its foal, respectively. Parameters with default values are described in Table 2.

Individuals younger than 1 year of age (hereafter referred to as foals) in addition acquire energy through suckling milk from their mother. Because of this milk suckling the model keeps track explicitly of all mother–child relationships, stopping milk production when either the mother or the foal dies or when the foal reaches one year of age. The maximum rate of milk production by adult females is assumed to be proportional to their total body mass, but this proportion declines with time passed since the birth of the foal (Table 1: Eqs. 10 and 14). Milk production is further reduced when foals are satiated, as we assume that milk production by mothers exactly matches milk intake by their foals. Like resource ingestion, milk intake is a sigmoid function of the reserves: total mass ratio $F:W$ of the foal, limiting the intake when reaching the target ratio. The energetic yield

ε_m for the foal and the costs σ_L for the mother per liter of milk are assumed to be constant (Table 1: Eqs. 10 and 14). We model foal ingestion as the sum of resource grazing and milk suckling without making further assumptions. In effect, this makes foals gradually switch from milk suckling to resource grazing during their first year of life, as a consequence of the decreasing milk production by the mother and the foal’s increasing energy demands due to growth.

Maintenance costs are assumed to scale following a three-quarters power law of total body mass W (Table 1: Eq. 11; Kleiber 1947, Reiss 1989, Flachowsky and Kirchgessner 1998, Brown et al. 2004). Energetic costs for growth are proportional to the rate of change in structural mass that follows from the von Bertalanffy growth curve (Table 1: Eq. 4). Energetic requirements

TABLE 2. Model parameters, with default values.

Parameter	Unit	Value	Description	Source
S_b	kg	25.5	structural mass at birth	1
S_m	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
β		0.56	fraction of females becoming pregnant	4
Δ_p	d	120	day in season that fetal development starts	4, 5
T_p	d	275	duration of fetal development period	4
ϕ_c	$kg\ kg^{-3/4}\cdot d^{-1}$	0.156	scalar constant in maximum grazing rate	2
ϕ_h	kg/ha	100	half saturation constant in grazing rate	6
η	kg^{-1}	15	steepness in satiation scaling of intake rate	7
σ_M	$MJ\ kg^{-3/4}\cdot d^{-1}$	0.6	scalar constant in metabolic costs	8
σ_G	MJ/kg	40	initial/fetal cost of structural mass growth	9
σ_L	MJ/kg	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/kg	1.9	milk energy content	10
ϵ_a	MJ/kg	54.6	anabolic reserves conversion efficiency	3, 11
ϵ_c	MJ/kg	39.3	catabolic reserves conversion efficiency	3, 11
μ_b	d^{-1}	3.86×10^{-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/ha	6000	maximum summer resource density	2
V_{min}	kg/ha	2000	minimum winter resource density	2
Θ		0.3	steepness in seasonality shift	13
χ_m	MJ/kg	10.7	resource energy content at start of summer	2
χ_s	d^{-2}	3.5×10^{-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

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, assumed in this study; 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).

per unit structural mass increase are assumed to increase with age (Table 1: Eq. 12) (Anonymous 1989). Analogously, for pregnant females, energetic costs for fetal development are proportional to the rate of change in structural mass following from the fetal growth curve (Table 1: Eq. 3), with a fixed proportionality constant σ_G (Table 1: Eq. 13). Finally, as discussed before, energetic costs of milk production for lactating females are proportional to the milk intake by their foals (Table 1: Eq. 14).

Dynamics of the reserves of an individual equals the balance of these various energy acquisition and expenditure processes and is different for the different types of individuals:

$$\frac{dF}{da} = \begin{cases} \epsilon^{-1}(I_R + I_M - C_M - C_G) & \text{for foals} \\ \epsilon^{-1}(I_R - C_M - C_G - C_P) & \text{for pregnant females} \\ \epsilon^{-1}(I_R - C_M - C_G - C_L) & \text{for lactating females} \\ \epsilon^{-1}(I_R - C_M - C_G - C_P - C_L) & \text{for pregant and lactating females} \\ \epsilon^{-1}(I_R - C_M - C_G) & \text{for males and other females.} \end{cases} \quad (17)$$

(For brevity all function arguments are suppressed in the above differential equation. We refer to Table 1 and the previous discussion for the definition of all component functions.) Depending on ingestion rates, reserves dynamics may be anabolic ($dF/da > 0$), in which case surplus energy ingested is stored, for example, in the form of adipose tissue. Alternatively, reserves may be used to cover the (fixed) energy requirements under conditions of resource scarcity, in which case reserve dynamics are catabolic ($dF/da < 0$). The parameter ϵ determines the conversion efficiency from reserves into energy, which is assumed different for anabolic ($\epsilon = \epsilon_a$; Table 2) and catabolic reserves dynamics ($\epsilon = \epsilon_c$; Table 2; Baxter 1989, Illius and O'Connor 2000).

Reproduction and mortality

We assume that every year a fraction β of all female individuals of 3 years and older are successfully inseminated (Garrott and Taylor 1990), independent of their reserves at that particular age and whether or not they are lactating. This assumption is corroborated by data of the Konik horse population (Vulink 2001). We assume that insemination takes place at the end of May/beginning of June, but that fetus development only starts some two months later (Kooijman 2000). In the

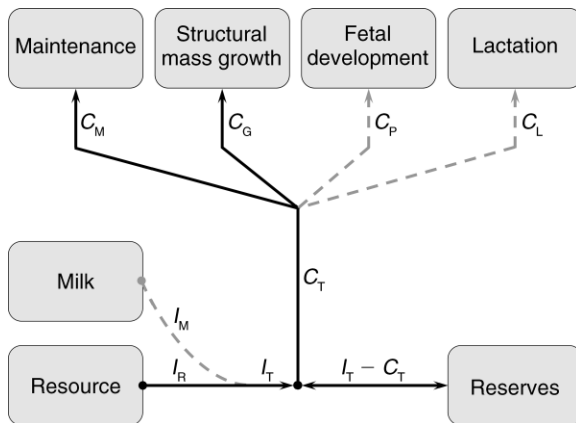


FIG. 1. Schematic overview of the individual energy budget. Energy acquisition processes are characterized by different intake rates I , while flows of energy expenditure are characterized by different rates C . Solid black lines represent energy flows that occur in all types of individuals independent of their age and sex. Energy flows occurring only in foals (I_M), pregnant (C_P), or lactating females (C_L) are indicated with gray dashed lines.

model we hence determine at day $\Delta_p = 120$ of each year for every female individual of 3 years and older with probability β whether or not she will carry a fetus. Fetus development is assumed to last for $T_p = 275$ days, after which period all pregnant females give birth simultaneously to their foals. This happens on day 31 of the year corresponding to 1 May. Foals are born with the same reserves: total body mass ratio as their mothers, whose reserves are reduced at birth by the amount of reserves provided to the foals.

Individual longevity is modeled with a Gompertz survival function (Table 1: Eq. 15), following Garrett and Taylor (1990). At birth every individual is assigned a uniformly distributed value between 0 and 1, which fixes their lifespan. Individuals die as soon as they have reached the age at which the value of the survival function drops below this randomly assigned value. We assume that individuals that are running low on reserves have an increased risk of mortality from other causes than old age, for example, due to reduced resistance against diseases. This additional, starvation-related mortality is modeled by a daily survival probability, which drops below 1 when the reserves: total mass ratio drops below a threshold value (Table 1: Eq. 16) and equals 0 whenever this ratio equals 0. For starving individuals every day a uniformly distributed value between 0 and 1 is drawn, which leads to death from starvation when it is larger than the survival probability $H_s(F, W)$ (Table 1: Eq. 16).

Resource productivity and dynamics

We assume resource productivity to be independent of current resource density on the grounds that vegetation regrowth is possible from plant parts not grazed by the ungulates. Hence, resource dynamics in the absence of

grazing follows semichemostat dynamics with a seasonally varying, maximum resource density $K(t_s)$ and turnover rate r (Table 2). Seasonal variation in maximum resource density is modeled with a modified sinusoidal function proposed by Turchin and Hanski (1997) (Table 1: Eq. 7) and parameterized for the particular system studied (Vulink 2001). Resource dynamics equal the balance between resource regrowth and grazing by all ungulate individuals, as described by the following differential equation:

$$\frac{dV}{dt} = r[K(t_s) - V] - A^{-1} \sum_i G_i(V, S_i, F_i, W_i). \quad (18)$$

In this equation A represents the surface area of the system studied (Vulink 2001), while the summation in the last term is over all individual ungulates alive.

Studying population dynamics

To investigate dynamics at the population level we use an existing framework for studying structured population models to keep track of the fate of all individuals in the population separately (De Roos et al. 1992). The latter methodology is based on a subdivision of the entire population into cohorts of individuals that have equal physiological properties and that develop throughout their lifetime without diverging. We adapted the methodology to account for all individuals in the population separately and to capture the discrete-event nature of birth and death processes. The most important reason to represent individuals separately, however, is the fact that pregnant and/or lactating adult females have different energy requirements than other individuals. The model explicitly keeps track of these demands as it follows each mother–foal relationship individually, stopping lactation when either the mother or the foal dies or when the foal reaches 1 year of age. Combined with the fact that females only reproduce with a certain probability each year, this leads to the situation that each adult female has her own unique history and current state of reserves dynamics, which can only be represented by following each individual separately. The resulting population model is therefore purely individual based (individual configuration models sensu Caswell and John 1992) with discrete birth and death events, but nonetheless continuous dynamics of resource and individual physiology.

Model variants

In addition to analyzing the baseline model with default parameters we studied two slightly extended model variants. To assess the influence of unpredictable weather conditions during winter we studied the influence of an uninterrupted period of snow cover. We assumed that during such a period of snow cover all grazing stops and individuals do not take in any resource. Furthermore, all resource regrowth was assumed to have stopped as well. We present results for a period of snow cover lasting 20 days, but results

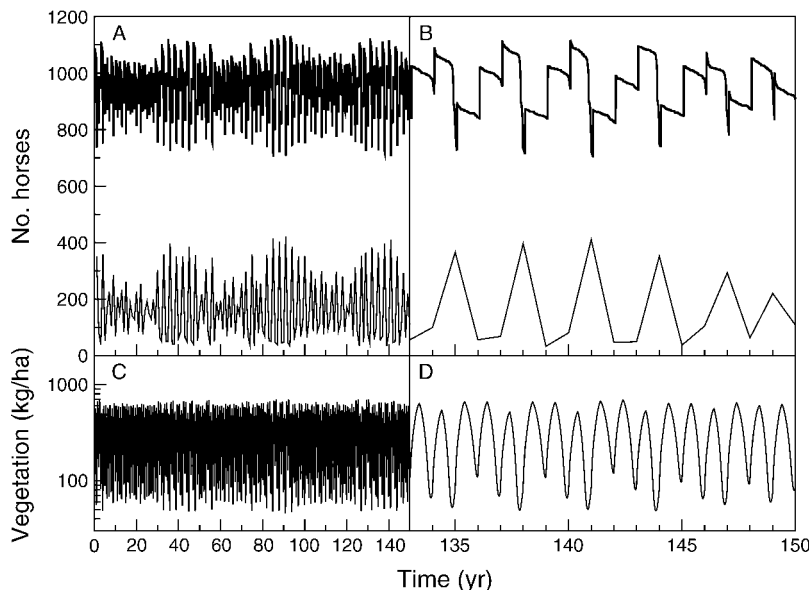


FIG. 2. Dynamics of the ungulate population as predicted by the baseline model with default parameters. (A, B) Total number of individuals in the population including foals, yearlings, and all older horses (upper line), and the cumulative number of deaths occurring during the entire year (lower line). (C, D) Vegetation density. Transient dynamics have been discarded. Panels B and D zoom into the last 15 of the entire period of 150 years to elucidate details of the dynamics.

with a 30-day period of snow cover are essentially similar. Whether or not a period of snow cover occurs is determined each year with a fixed probability. The period of snow cover is assumed to start at day 300 of the year corresponding to 1 March. This timing is expected to affect the population dynamics most because of reduced individual conditions due to poor feeding during the preceding winter months.

To analyze how density dependence in reproduction would affect population dynamics we investigated a model variant in which the pregnancy probability depends on the female body condition at insemination. Instead of a fixed probability β (see Table 2), we assume that insemination will not lead to successful pregnancy if the reserves:mass ratio F/W of the female individual is below the threshold ρ_s that marks the onset of starvation mortality (see Table 2). Above this threshold we assume the pregnancy probability to increase linearly with the female reserves:mass ratio from a value of 0 when $F/W = \rho_s$, to the default value β for the maximum reserves:weight ratio $F/W = \rho$.

RESULTS

Baseline dynamics

Fig. 2 shows the long-term dynamics of the ungulate population over a period of 150 years as predicted by the baseline model with default parameters. Transient dynamics have been omitted. The figure also highlights in detail the dynamics over the last 15 years of the simulation period (right panels). On average the ungulate population consists of roughly 1000 individuals, which keep the resource density at a level far below

its maximum. When considered over a longer time period fluctuations in ungulate and resource densities appear irregular. Periods with more regular, large-amplitude oscillations in the ungulate density alternate with periods during which oscillations are more erratic and of smaller amplitude. The pattern is most clearly visible in the cumulative number of deaths occurring during an entire year (Fig. 2A, B). The detailed dynamics shown in the right panels of Fig. 2 reveal that the more regular fluctuations have a periodicity of three years and are characterized by a distinct pattern in the number of individuals dying, with two years of low death tolls followed by a single year with large numbers of dying individuals (Fig. 2A, B). As a result, the total number of individuals increases in a stepwise manner during three reproduction pulses, followed by a large die-off of individuals in the winter following the last of these reproduction events. The maximum number of individuals in the population and the number of individuals dying in the large die-off varies from period to period. In addition, due to demographic stochasticity the period of the regular pattern is sometimes disrupted (e.g., at $T = 149$ in Fig. 2), which makes the dynamics appear irregular when viewed over longer time periods. Despite these irregularities, inspection of the autocorrelation in total ungulate density clearly reveals a basic dynamic pattern with a periodicity of three years (autocorrelation at lag 3 measured over 10 simulations: 0.73 ± 0.05 [mean and standard deviation]).

We carried out 10 different simulations of the population dynamics over a 1000-year period. We discarded transient dynamics by only measuring popu-

TABLE 3. Mean total population size, number of births and deaths, and variation therein (coefficient of variation, minimum and maximum value observed) for different probabilities of a period of 20 days snow cover occurring toward the end of the winter.

Probability of snow	No. in total population				No. total births				No. total deaths			
	Mean	CV (%)	Min.	Max.	Mean	CV (%)	Min.	Max.	Mean	CV (%)	Min.	Max.
0.0	1003	7.9	818	1156	165	8.7	122	209	165	78.3	26	481
0.2	995	8.0	780	1155	164	8.8	121	211	164	78.2	26	508
0.5	983	8.3	764	1149	163	9.0	120	210	163	80.9	24	522
0.8	975	7.9	777	1138	162	8.6	119	206	162	78.4	25	498

Note: All statistics represent averages measured over the last 900 years of 10 simulations over a period of 1000 years.

lation statistics over the last 900 years of each simulation. Table 3 (first row) presents the results of these simulations in terms of total population size, number of foals born, and the number of individuals dying per year. Both average values and the variation in these statistics (CV, minimum and maximum value observed) over the 900-year measuring period are presented. As the most remarkable feature of these results, the coefficient of variation (CV) of the number of individuals dying each year is roughly an order of magnitude larger than the CV of the total population size and the number of foals produced yearly. This high CV value for the number of deaths results from the periodic pattern shown in Fig. 2, with a heavy death toll occurring roughly every three years, separated by two consecutive years with relatively low numbers of individuals dying. By expressing the number of individuals dying in a given year as a percentage of the total population size at the beginning of the year, we constructed a frequency distribution of the observed death toll per year (Fig. 3). This frequency distribution turns out to have a bimodal shape with a large peak at low death tolls (5–10% of the individuals dying in a year)

and a second peak at high death tolls (>30% of the individuals dying in a year). On the basis of this frequency distribution we distinguish between “collapse” years with a large die-off of individuals (>20% of the population) and “noncollapse” years (<20% of the population is dying). Using this distinction, roughly 34% of all years are classified as collapse years, in accordance with the three-year periodicity of the basic dynamic pattern.

Fig. 4 shows the survival probability for differently aged individuals in collapse and noncollapse years. In noncollapse years individuals between 2 and 20 years of age have roughly similar survival probabilities and mostly die because of background mortality. The survival probability of older individuals is smaller as they suffer from senescence. Foals also have a somewhat smaller survival probability than individuals aged between 2 and 20 years, probably because in addition to background mortality they also die from lack of milk intake whenever their mother dies. Yearlings aged between 1 and 2 years old, however, have the lowest survival probability of all.

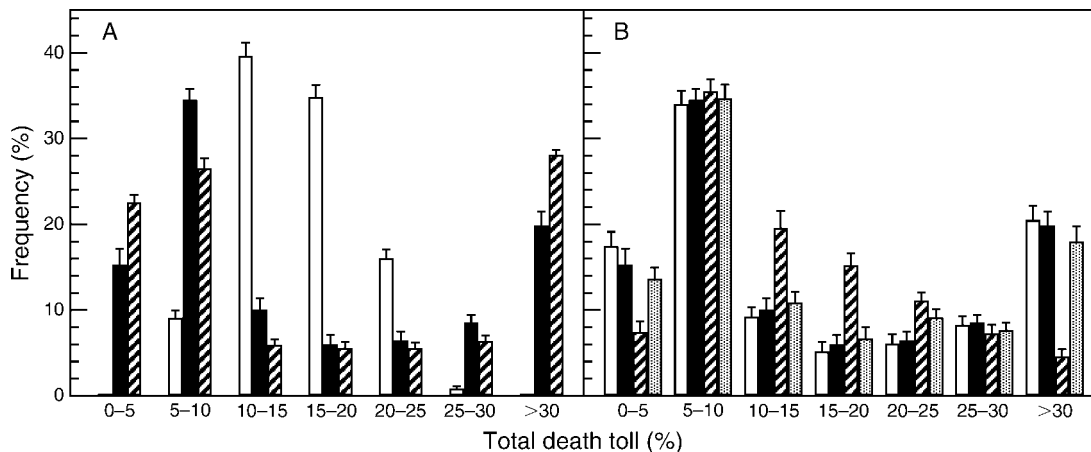


FIG. 3. Frequency distribution of the yearly death toll, when expressed as a percentage of the total population size at the beginning of the year. In both panels the distribution for the baseline model with default parameters (cf. Fig. 2) is shown for reference (solid bars). (A) Baseline model predictions with half ($V_{\min} = 1000$, $V_{\max} = 3000$; open bars) and double ($V_{\min} = 4000$, $V_{\max} = 12000$; hatched bars) the default value for maximum resource density. (B) Model variant with a 50% probability of 20 days of snow cover each year (open bars), and model variant with condition-dependent fecundity with default value $\beta = 0.56$ (cf. Fig. 7; hatched bars) and adjusted value of $\beta = 0.75$ (cf. Fig. 7; stippled bars). Data represent averages and standard deviation of 10 simulations, each covering a period of 1000 years. The frequency distribution of the total death toll was measured over the last 900 years in each simulation.

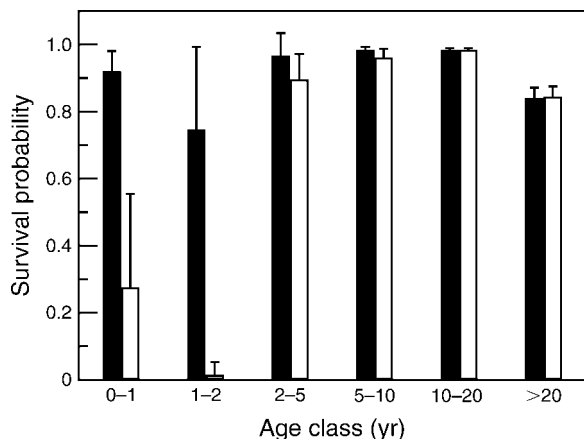


FIG. 4. Fraction of the different age classes of individuals dying during years of a population collapse (open bars) and during other years (filled bars) as predicted by the baseline model with default parameters (cf. Fig. 2). Collapse years are defined as years when >20% of the population dies. Data represent averages and standard deviation of 10 simulations, each covering a period of 1000 years. The age-dependent survival probability was measured over the last 900 years in each simulation.

Fig. 5A shows that in an absolute sense the energy demands to cover growth in structural mass are largest between 1 and 2 years of age. Absolute energy requirements, however, do not correctly reflect vulnerability to starvation, as individuals of different sizes also have different amounts of energy reserves. In the absence of any food intake the ungulate reserves dynamics is described by the following differential equation:

$$\frac{dF}{dt} = - \frac{[\sigma_M(S + F)^{3/4} + D]}{\epsilon_c}$$

In this equation the first term in the numerator represents maintenance costs and the constant D

represents all other energy demands (cf. Eq. 17). Using Maple, this differential equation can be solved explicitly (solution not shown) to compute the time it takes to deplete the reserves F to the threshold ρ_s , below which starvation mortality is nonzero, when starting from an initial reserves : mass ratio equal to the maximum $F/W = \rho$. Fig. 5B shows the time until the onset of starvation in case only energy requirements for maintenance are taken into account [$D = 0$], and in case energy demands for growth in structural mass are also considered [$D = C_G(a, S)$]. Irrespective of whether growth costs are taken into account, the time period until the onset of starvation increases with individual body size. On the basis of purely energetic considerations, one would hence expect foals and not yearlings to be most vulnerable to starvation mortality. To some extent the higher vulnerability of yearlings arises because they do not profit from additional energy intake through suckling and rely completely on resource grazing for their energy intake. Most importantly, however, foals have the advantage to be born with a relatively high reserves : mass ratio, which equals their mother's, whereas yearlings are burdened by a significantly lower body condition than foals at the start of summer. Foals suffer depletion of body reserves during their first winter because of their growth demands (Fig. 6), and hence start their second summer with a significantly lower reserves : mass ratio than they were born with. Yearlings remain affected by this legacy of their first winter starvation period, as the difference persists during the remainder of summer. The following winter the difference results in yearlings entering starvation mortality earlier than foals (Fig. 6), which causes them to suffer higher mortality and explains their lower survival probability.

In collapse years the survival probability of yearlings is virtually 0 (Fig. 4), while the survival probability of foals is significantly lower as well. In some collapse years all individuals from both youngest cohorts die (Fig. 6; $T = 139$ and $T = 143$), while in other collapse years a

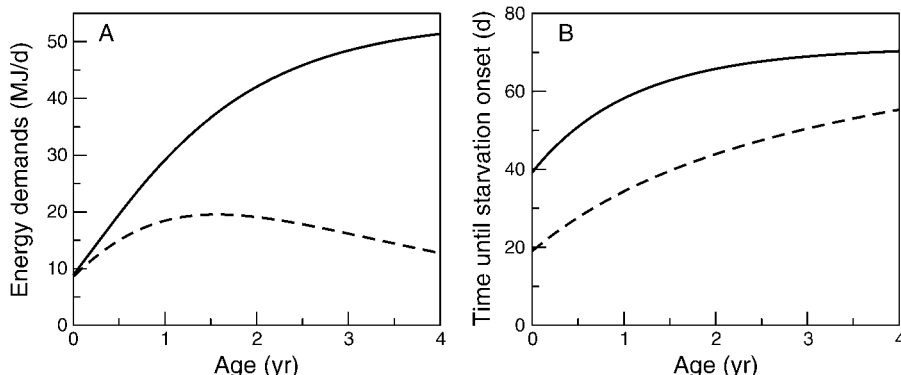


FIG. 5. (A) Energetic demands at various ages required to cover maintenance of an individual with optimal reserves : mass ratio (solid line) and to cover the costs for growth in structural mass (dashed line). (B) Time required to deplete reserves to the reserves : mass threshold ρ_s below which starvation mortality starts, when starting from an optimal reserves : mass ratio. The solid line indicates the case of negligible energy demands for growth in structural mass; the dashed line shows the case including energy demands for growth in structural mass at every age (cf. panel A).

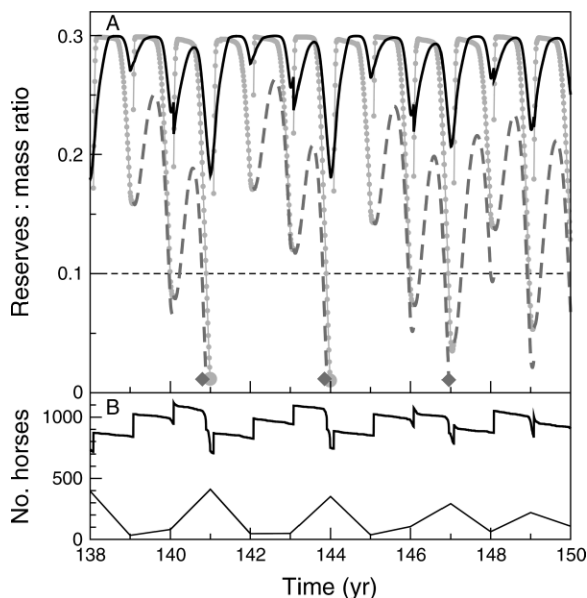


FIG. 6. Dynamics of the reserves : mass ratio during the last 12 years of the population dynamics shown in Fig. 2. (A) Dynamics of the reserves : mass ratio of foals (light-gray lines with circles), yearlings (dashed, dark-gray line), and all other individuals (solid black line). Breaks in the lines for the foals and yearlings occur at the moment that the current cohort progresses to the next age class, and the following data represent a new cohort of foals and yearlings. Light-gray circles and dark-gray diamonds indicate the times that an entire cohort of foals or yearlings, respectively, has died out. (B) Total number of individuals in the population including foals, yearlings, and all older horses (upper line), and the cumulative number of deaths occurring during the entire year (lower line) as also shown in Fig. 2B, D.

number of foals still survive (Fig. 6; $T = 146$ and $T = 148$). Yearlings almost never survive during a collapse year (but see Fig. 6; $T = 148$). Considered over the lifetime of a single individual, its reserves : mass ratio is lowest at the end of its second winter (Fig. 6). This dip in the body condition carries over to its third summer, during which its condition slowly recovers if population densities are not too high and vegetation is relatively abundant. During collapse years, however, population densities are so high and competition so intense that the condition of individuals between 2 and 3 years of age does not recover sufficiently and leads to some starvation mortality the following winter. For this reason the survival probability of individuals between 2 and 5 years of age is slightly lower in collapse years than during noncollapse years. In contrast, survival of individuals of 5 years and older is not significantly different in collapse and noncollapse years (Fig. 4).

Summarizing, the intrinsic dynamics of the ungulate population under these conditions is characterized by a dynamic pattern with an alternation between years with low death tolls and years with heavy death tolls. This dynamic pattern arises as a consequence of increasing ungulate densities overexploiting the resource to such an extent that foals and yearlings enter starvation condi-

tions during winter. Once every three years this results in an almost complete eradication of the yearling class and a significant decimation of the foal age class. After a collapse year, the population expands over a period of three years to densities that overexploit the resource once again. Although all individuals in the population suffer from density dependence, the energy demands for growth result in foals and yearlings being more vulnerable to starvation than older individuals, while yearlings suffer more than foals due to their poorer reserves status. This age-dependent vulnerability to starvation also results in a punctuated age composition of the population, such that the age distribution consists of an alternation of a single abundant and two consecutive missing year classes (results not shown). This clustered age distribution in turn contributes to the oscillatory behavior, as it implies that recruitment to the adult class varies over time.

We have found that the characteristic dynamic pattern with an alternation between collapse and non-collapse years is more pronounced at higher productivity levels of the resource. Our default parameters imply that resource productivity varies from 4 kg/ha in winter to 12 kg/ha in summer, which allows the persistence of a population with on average 1000 individuals. Since this density roughly corresponds to the densities observed in the nature reserve that the model is parameterized for (Vulink 2001, Anonymous 2004), we conclude that our default parameters correctly reflect the average system's productivity of resources that are available for the ungulates to forage on. If we assume the average system productivity to be half the default value, while keeping the ratio between winter and summer productivity the same ($V_{\min} = 1000$, $V_{\max} = 3000$), the characteristic alternation between collapse and non-collapse years disappears. Although the autocorrelation of the total ungulate density is still indicative of a three-year periodicity (autocorrelation at lag 3: 0.57 ± 0.02), the frequency distribution of the yearly death toll now has a unimodal shape, and shows that each year 10–20% of the population dies (Fig. 3; left panel). Both good (with <10% of the population dying) and bad (>20% dying) survival years are scarce and the year-to-year variability in yearly death toll is smaller. In contrast, doubling the average system productivity, while keeping the ratio between winter and summer productivity the same ($V_{\min} = 4000$, $V_{\max} = 12000$), strengthens the characteristic pattern with alternation between collapse and non-collapse years. The frequency distribution of the yearly death toll is more bimodal than for default parameters (Fig. 3; left panel), especially because the occurrence of years during which >30% of the population dies, increases, while the number of years during which between 5% and 30% of the population dies decreases. Because the frequency of years with 5–10% mortality decreases to the same extent as the frequency of years with 0–5% increases, it can be argued that the years with good survival become even better at higher productivity,

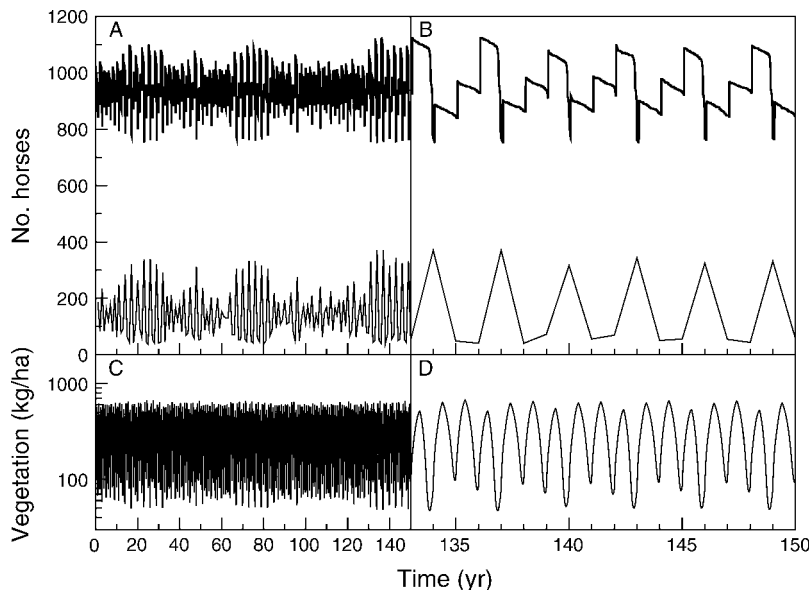


FIG. 7. Dynamics of the ungulate population for the case when the probability of insemination depends on the current body condition of the female (cf. Fig. 2). (A, B) Total number of individuals in the population including foals, yearlings, and all older horses (upper line), and the cumulative number of deaths occurring during the entire year (lower line). (C, D) Vegetation density. Transient dynamics have been discarded. Panels B and D zoom into the last 15 years of the entire period of 150 years to elucidate details of the dynamics. The default parameter values have been used.

while the bad ones get worse. The autocorrelation of total ungulate density in this case not only reveals a three-year periodicity (autocorrelation at lag 3: 0.31 ± 0.01), but also a five-year periodicity (autocorrelation at lag 3: 0.36 ± 0.06). The high productivity levels lead to high population densities, which more rapidly expand to levels where they overexploit the available resources. Hence, the population dynamics in this case reveals that sometimes a population collapse already occurs after two years of expansion, which is usually followed by a three-year period during which the population expands and collapses. The latter alternation explains the five-year periodicity in the autocorrelation function.

Effect of periods with snow cover

As described for the baseline model we also carried out 10 different simulations of the population dynamics over 1000-year periods with the model variant in which every year, with a particular probability, a 20-day period of snow occurred starting at day 300 of the season (1 March). Snow cover is assumed to completely prevent both resource regrowth and ungulate grazing. Transient dynamics were discarded, as before. Table 3 summarizes the results of these simulations in terms of total population size, number of foals born, and the number of individuals dying per year (average, minimum, and maximum value observed and CV). The results reflect our general finding that independent of its probability of occurrence, a period of snow cover does not affect the baseline dynamic in any major aspect. The autocorrelation function of total ungulate density is again indicative of a three-year fluctuation period (50%

probability of snow cover; autocorrelation at lag 3: 0.55 ± 0.05). The frequency distribution of the death toll in terms of the percentage of individuals dying in a year is also not affected by the occurrence of a period of snow cover (Fig. 3B). Fig. 5B shows that the energy demands for growth significantly shorten the time until the onset of starvation mortality, but that all individuals can sustain at least a 30-day period without food when their energy reserves at the start of the period are maximal. Therefore, in noncollapse years when individual body conditions are not significantly reduced by deteriorating food conditions, a period of snow cover will not significantly reduce the survival probability of the various age classes in the population. In collapse years the snow cover will expedite the extinction of the foal and yearling cohorts, but they would also have died without the snow cover. As a consequence, snow cover does not significantly change the baseline dynamics of the ungulate population.

Condition-dependent reproduction

Fig. 7 shows the population dynamics for the case when the probability of pregnancy depends linearly on the reserves:mass ratio of the mother at the time of insemination, starting at 0 for $F/W = \rho_s$ and rising to β at $F/W = \rho$. As for the baseline model, Fig. 3 presents the frequency distribution of the death toll in terms of the percentage of individuals dying in a year. Characteristics of the population dynamics are, as before, measured over the last 900 years of 10 replicate simulations covering a total period of 1000 years. The condition-dependent fecundity does not qualitatively

change the basic three-year pattern that characterizes the baseline dynamics (compare Fig. 2 with Fig. 7), as shown by the autocorrelation function of total ungulate density (autocorrelation at lag 3: 0.74 ± 0.03). The pattern of age-dependent survival in collapse vs. non-collapse years is also similar to the pattern shown in Fig. 4 for the baseline model dynamics. However, the condition-dependent fecundity does reduce the occurrence of collapses of the population, in which $>25\%$ of the individuals die (Fig. 3). Instead, population declines of between 10% and 25% during a year occur more often.

The condition-dependent fecundity reduces the average number of foals produced each year, because individuals always have a reserves:mass ratio which is lower than its maximum value (Fig. 6). The pregnancy probability is hence always smaller than β . On average 41 foals are produced every year per 100 adult females in the baseline model, while in the case of condition-dependent fecundity, only 33 foals are produced. Assuming a higher value for β than the default we can compensate for this decreasing effect of condition-dependent fecundity on the average number of foals produced. With $\beta = 0.75$ the average fecundity is similar to that of the baseline model with default parameters (41 foals per 100 adult females). At the same time, the frequency distribution of death tolls regains its bimodal shape with this higher value of β and closely resembles the distribution observed for the baseline model with default parameters (Fig. 3). We hence conclude that it is the decrease in average fecundity and not the change in fecundity with body condition that causes population collapses, in which more than 25% of the individuals die, to occur less frequently (Fig. 3). Because of the lower fecundity, the overshoot of the population is less pronounced, leading to less severe overexploitation of the resource and smaller collapses. Otherwise, dependence of fecundity on year-to-year variability in reserves:mass ratio at the time of insemination does little to buffer fluctuations in population density.

DISCUSSION

On the basis of our analysis, competition for resources permits, on average, only every third year-class of newborns in a Konik horse population to survive in considerable numbers and contribute to future generations. These successful year-classes, which are born right after the population has decreased to relatively low densities, hence dominate and make up the largest part of the entire population. The intervening two year-classes experience high death rates as foals and yearlings and are basically wiped out during the years of a population collapse. During a collapse almost all yearlings die, while some 75% of the foals perish as well. Yearlings suffer more than foals mostly because they are burdened with the legacy of their first winter starvation period, during which they developed a shortage of reserves, while still having considerable

energy demands for growth in structural mass. The disappearance of two consecutive year-classes creates a hole in the population age structure, which results in a lack of recruitment to the adult population for two consecutive years and gives rise to the oscillations in population abundance.

Population dynamics and especially population feedback on resources therefore determines life history of individual ungulates that are born in different years and hence experience different population densities during their initial development. As a consequence, we expect ungulate populations to exhibit an alternation between years with a relatively low death toll, in which $<10\%$ of the individuals die, and collapse years with $>30\%$ of the population dying. These collapse years result from the intrinsic dynamics of the population, in particular intraspecific differences in vulnerability to resource overexploitation, and occur independent of environmental conditions. They are, however, more likely to occur at high resource productivity even though this change in productivity does not significantly change population fecundity (roughly 41 foals per 100 adult females at both low and high productivity). Our results agree with earlier findings that ungulate population dynamics are mostly influenced by density dependence in juvenile survival (Gaillard et al. 1996, Loison et al. 1999) rather than by density dependence in fecundity (Bonenfant et al. 2002). In contrast, we did not find a significant effect of a period of snow cover during winter on dynamics (Coulson et al. 2000, Forchhammer et al. 2001), which we could explain in terms of the underlying energy budget processes and the amount of reserves of well-fed individuals.

Previous modeling studies have used more aggregated models, such as matrix models (Eberhardt 1991, Grenfell et al. 1992), simple predator-prey models (Owen-Smith 2002), or differential equation models representing age- and sex-classes (Illius and Gordon 1999, Illius and O'Connor 2000) to analyze ungulate dynamics. In contrast, we used an individual-based, structured population model, based on a core representation of the individual energy budget and life history. Consequently, this model is rather complex and detailed, and therefore necessarily tailored to a particular system. Only such an individual-based model, however, allows us to unravel the complete and two-way interrelationship between individual life history and population dynamics. This advantage can be appropriately clarified by a comparison with the study of Grenfell et al. (1992). Using a matrix model, these authors showed that highly overcompensating density-dependent mortality can generate recurrent population crashes occurring roughly every three years, which are consistent with those observed in a naturally limited population of Soay sheep. In other words, by assuming both the form and strength of density dependence, these authors revealed how aspects of individual life history shaped population dynamics. As we argued in the *Introduction*, however, this is only one

leg of the interrelationship between life history and population dynamics, as population dynamics in turn shape life history through density dependence. Our individual-based population model does not explicitly or a priori assume a specific form of density dependence. Rather, the density-dependent influence on juvenile survival emerges as a result of an interaction between the population feedback on resources and the mechanistic model of individual energetics and life history. By the same token, before analyzing the model results we considered density dependence in reproduction just as likely to emerge, given that pregnancy and lactation represent considerable energy demands that increase the risk of starvation for pregnant and lactating females. An individual-based, structured population model, based on a core representation of individual energetics and life history, reveals the ultimate effect and strength of density dependence on different aspects of individual life history, and hence unravels both legs of the interrelationship between life history and population dynamics. The strength of this approach is illustrated by the relationship that we revealed between age-dependent survival in collapse years and size-dependent energy requirements, as well as by the explanation for the insensitivity of dynamics to snow conditions during winter in terms of depletion times of individual energy reserves.

Although our population model has a general structure, we parameterized it for a particular system, the Konik horse population in the Oostvaardersplassen (OVP) in the Netherlands. This nature reserve is a highly productive wetland (Vulink 2001), which sustains a population of roughly 1000 Konik horses in addition to populations of Heck cattle and red deer. The population has recently been the subject of a public debate about the likelihood and naturalness of large die-offs during winter (ICMO 2006). For simplicity we did not account for any competition among the three grazer populations, and simply assumed that only part of the resources were available for the horse population independent of the other two grazers. The model predictions regarding the total population size are in close agreement with the currently observed abundance of Konik horses. Given the rather high density in a productive environment, we would expect population collapses, in which 20–40% of all individuals die, to occur regularly. The grazer populations in the OVP were introduced in the early 1980s, and hence were below carrying capacity for most of the last 30 years (ICMO 2006). High death tolls are likely to occur more frequently in the years to come (ICMO 2006), but as of yet have only been observed for Heck cattle (five times, with a range of 20–35% in the last 10 years; F. Vera, *personal communication*), and are starting to emerge for Konik horses (reaching >20% for the first time in 2007; F. Vera, *personal communication*). On the basis of our model results, however, we expect population collapses exceeding 40% of the population to be unlikely. Observations on the Konik horses in the OVP show that mortality mostly affects the young

individuals that fail to survive their second winter (F. Vera, *personal communication*). The latter observation is in line with our model predictions that yearlings, particularly, are at risk of starvation.

As the most novel result, our analysis suggests a potential, mechanistic explanation for the observed high mortality among horses in their second winter, which we argue results primarily from the reduced body condition developed by yearlings during their first winter. Density-dependent, overcompensating juvenile mortality has often been identified as an important driver of population fluctuations in ungulates (e.g., Gaillard et al. 1996, Loison et al. 1999). However, the mechanism that gives rise to this mortality, be it the relatively high energetic requirements for growth in juveniles, or their poorer reserve status at the beginning of winter, is less well established. It has been argued elsewhere that these causes can only be revealed by the type of individual-based, mechanistic modelling presented here (Illius and Gordon 1999:417–418). Our results resemble the findings of Clutton-Brock et al. (1997), who showed that fluctuations of the Soay sheep population of Hirta (St. Kilda) resulted from overcompensatory winter mortality, and that the interplay between individual energetics and population feedback is more likely to give rise to density dependence in mortality, rather than in fecundity. Illius and Gordon (1999) concluded that this lack of density dependence in fecundity of Soay sheep results from the high rate at which female fat mass recovers after pregnancy and lactation. On the basis of our results, a similar conclusion can be postulated for Konik horses, as we also have not observed any increase in mortality of pregnant and lactating females, despite the fact that the energetic costs involved are substantial. In contrast to Konik horses, however, winter mortality among Soay sheep occurs mainly among lambs, whereas mortality of yearlings and adults does not differ significantly. Clutton-Brock et al. (1997) argue that lambs are more at risk than older individuals because of their smaller body fat reserves and their higher energy expenditure in thermoregulation. Illius and Gordon (1999), furthermore, show that male yearlings and adults experience stronger density dependence in mortality than female yearlings and adults, because of their larger energy investment into rutting behavior. In contrast to Soay sheep, population dynamics of the deer population on the Isle of Rhum has been argued to exhibit more stable dynamics due to a lower fecundity and slower maturation (Clutton-Brock et al. 1997). Accordingly, our results also reveal that a lower average fecundity reduces the magnitude of the population collapses, even though the basic dynamic pattern is not changed.

Oscillations related to population age, stage, or size structure are a well-known phenomenon, occurring in a wide variety of species (Gurney et al. 1980, Murdoch and McCauley 1985, Hamrin and Persson 1986, Godfray and Hassell 1989, Murdoch et al. 2002). Persson et al. (1998; see also De Roos and Persson 2003) show that

such cycles may arise in populations with yearly reproduction when offspring cohorts suffer more from competition for resources than their parents and hence go extinct shortly after birth. These cycles resemble the population fluctuations we found, but in contrast to being less effective competitors for resources, young individuals in our model have higher energetic demands due to their prescribed growth in structural mass. Nonetheless, as in the study by Persson et al. (1998), the more precarious energy balance of juveniles compared to adult individuals makes them suffer to an unequal extent from resource scarcity. This asymmetry is one, if not the most important, mechanism causing the fluctuations in ungulate density (see also De Roos and Persson 2003).

Prescribed growth in body size sets our energy budget model apart from earlier energy budget models (Kooijman and Metz 1984, Gurney et al. 1990, Persson et al. 1998, Kooijman 2000, Lika and Nisbet 2000), in which food acquisition is always the limiting process rate, determining the rate of both growth and reproduction. In contrast, in our energy budget model demands are fixed and independent of current food availability. Fixed energy demands require that they have to be covered from stored reserves in case of food scarcity and that food acquisition is limited by factors other than food density under conditions of ample food supply. Otherwise, the latter may initiate a runaway process of reserves build-up. We assumed food intake rate to be dependent on the current reserves:mass ratio of the individual, limiting intake when this ratio approached a set target value. As discussed above, the population dynamics revealed in this paper resemble the type of population cycles investigated by Persson et al. (1998), despite the structural difference in energy budget model. This resemblance supports the claim of De Roos and Persson (2003) that intraspecific interactions among individuals with different physiological status are a key factor shaping population dynamics more than details of individual energetics.

We have not been able to establish whether or not feral horse populations exhibit the predicted, three-year cycles due to a lack of population dynamic data over sufficiently long time periods. Cyclic dynamics with a three- or four-year period have been shown to occur in Soay sheep (Clutton-Brock et al. 1997) and in musk ox populations in certain regions of Greenland (Murdoch et al. 2002). Nonetheless, the discrepancy that models of ungulate dynamics readily predict population cycles (Grenfell et al. 1992, Illius and Gordon 1999, Owen-Smith 2002), but clear cycles are only observed in few cases, raises the question of which types of mechanisms might counter the inherent tendency to oscillatory dynamics in ungulates. Heterogeneity in the vegetation has been suggested as a possible explanation for the stabilization of ungulate dynamics (Owen-Smith 2002), although this mechanism seems less relevant for populations of hindgut fermenters such as Konik horses,

given their wide array of forage species (Vulink 2001). Other stabilization mechanisms might include behavioral responses to vegetation changes due to optimal foraging (Fryxell 1991) or monopolization based on dominance hierarchies. Lastly, interactions with pathogens or predators (Wilmers et al. 2006) may dampen irruptive dynamics in ungulates. Although not relevant in our study system, predation may especially stabilize dynamics in case it targets small, young prey individuals (Sinclair et al. 2003), killing them before they die of starvation. In this paper we reveal how population dynamics shapes individual life history plus density dependence therein, and thus intrinsically induces fluctuations. Investigating which mechanisms can subsequently stabilize them, we consider a question for further research.

Contrasting the dynamics of two populations of food-limited ungulates (red deer and Soay sheep) on different Hebridean islands, Clutton-Brock and Coulson (2002) concluded that the devil is in the details and that small differences in the individual life history may give rise to significantly different dynamics. Indeed one could rightfully pose the question to what extent our model results generalize to different species of ungulates in other circumstances. While formulating the model, we have made assumptions that are specific for the particular species and system we study. The type of analysis we present, however, illustrates an inductive approach to the study of ungulate population dynamics, which adds to the more deductive approach using time series analysis. The approach allows the unraveling of how individual-level energy budget dynamics and other life history processes translate to the population level and shape ungulate population dynamics, which in turn shape individual life history through density dependence and feedback of population grazing on resources. The use of structured population models based on a core model of individual energetics and life history therefore allows for developing a qualitative, mechanistic understanding of the complex and two-way interrelationship between individual life history and population dynamics, which can subsequently be used to speculate how species-specific differences might shape life history and population dynamics in other systems. We consider this mechanistic understanding more important and more likely to allow generalizations than the model itself. For example, on the basis of our results we speculate that species with a more rapid growth and shorter juvenile periods will tend to fluctuate less, unless other factors, such as high fecundity, exacerbate the oscillatory tendency. Also, we do not expect social interactions to play a major role in stabilizing population fluctuations, as it is unlikely that juvenile individuals will be sufficiently dominant to monopolize a large enough part of the resources to prevent their starvation. In fact, dominance hierarchies may even accentuate population cycles if, as a consequence, juvenile individuals get less than their fair share of available resources.

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