

ARTICLE

Shifting seasonality of annual growth through ontogeny for red deer at northern latitudes

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Abstract

Large mammals at northern latitudes show annual cycles of body mass gain in summer and body mass loss in winter. The amplitude and seasonal timing of these cycles may vary through ontogeny depending on trade-offs toward investments in structural growth versus fat storage, reproduction, and future survival. Despite this knowledge, there is no detailed model of how the seasonality of body mass develops through ontogeny. Here, we define a new seasonal growth model that accounts for shifting seasonality through two sine components: one included in the growth coefficient and the other on the asymptotic size. We fitted 12 candidate models to longitudinal data on body mass of captive male and female red deer (*Cervus elaphus*) in Norway, with different baseline growth structures (von Bertalanffy, Gompertz, and Brody) and including zero, one, or both of the seasonal components. The best fitting model was the Brody model with both seasonal components included, allowing the annual peak to shift through ontogeny: The annual peak occurred in December for calves, shifting to November in yearlings, and October in 2- and 3-year-olds, ending with September for adults. All age classes showed an annual minimum at the end of winter around March. Males and females showed similar seasonal peaks through ontogeny, although males grow bigger and have larger seasonal amplitudes. Our new growth model provides a flexible framework to model seasonal growth changing through ontogeny, applicable to different species.

KEYWORDS

Brody, Gompertz, growth model, ontogenetic shift, red deer, seasonal growth, seasonality, ungulates, von Bertalanffy

INTRODUCTION

Animals show different adaptations to cope with seasonal variation in the environment (Telfer & Kelsall, 1984), including hibernation, food, or fat storage. At northern latitudes, ungulates experience large seasonal variation in the

quality and abundance of plant forage, and low forage availability coincides with harsh climatic conditions (Moen, 1976, 1978). This gives rise to annual cycles of body mass gain in summer and body mass loss in winter, and the annual fat cycle is the key to understanding their ecology (Mautz, 1978; Parker et al., 2009). These annual cycles of

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body mass also vary through ontogeny from calf to adulthood depending on trade-offs toward investments in structural growth versus fat storage, reproduction, and future survival (Festa-Bianchet et al., 1998; Green & Rothstein, 1991). Young animals invest more available energy in structural body growth and less in fat storage compared with adults. After age at first maturation, sub-adults continue to invest in structural growth, while adults invest more heavily in reproduction alone at the expense of further growth (Weladji et al., 2010). These trade-offs in investments to structural growth and storage are key to an improved understanding of age- and sex-specific differences in survival and reproduction under variable environmental conditions (Gaillard et al., 2000; Toïgo & Gaillard, 2003).

Despite the common knowledge of the annual cycles of body mass in ungulates and many other mammals, there is surprisingly little quantitative information available on whether and how the seasonal fluctuations in body mass develop through ontogeny. Most studies of intra-annual changes in body mass in ungulates at northern latitudes are based on data sets with only two time points per year, spring and fall, as in mule deer (*Odocoileus hemionus*) (Monteith et al., 2013), moose (*Alces alces*) (Van Beest & Milner, 2013), reindeer (*Rangifer tarandus*) (Albon et al., 2017), and bighorn sheep (*Ovis canadensis*) (Festa-Bianchet et al., 1996; Pelletier et al., 2007). More detailed temporal data on intra-annual body mass changes have been shown for red deer (*Cervus elaphus*) (Mitchell et al., 1976), roe deer (*Capreolus capreolus*) (Mauget et al., 1997), reindeer (Tyler, 1987), and fallow deer (*Dama dama*) (Weber & Thompson, 1998), but these studies did not fit any seasonal parametric growth model. For black-tailed deer (*O. hemionus*), seasonal data were shown for growth, while the fitted growth model was only annual (Bandy et al., 1970). Seasonal growth models have been fitted for sika deer (*Cervus nippon*) in Japan (Suzuki et al., 2001), for reindeer introduced to South Georgia (Leader-Williams & Ricketts, 1982), and for white-tailed deer (*Odocoileus virginianus*) from birth to maturity (Moen, 1978); however, these models did not account for the potentially shifting seasonality of body mass through ontogeny. Fitting such models require repeated individual size measurements throughout ontogeny and seasons. Most datasets that meet these requirements are only available for captive populations.

Here, we develop seasonal growth models of body mass with fixed or shifting seasonality through ontogeny, using sine function components. The seasonal models are defined for three classical baseline growth models for mass at age: the von Bertalanffy model (von Bertalanffy, 1957), the Gompertz model (Winsor, 1932), and the Brody model (Brody, 1945). Our growth models and statistical approach provide a useful framework to study seasonal growth that

potentially shifts with age. Using longitudinal data on red deer, we compare fitted growth models to test two competing hypothesis: The fixed seasonality hypothesis (H0) predicts a constant timing of seasonality in summer mass gain and winter mass loss across ontogeny, as all animals experience the same seasonal variation in environmental conditions. We tested this against the shifting seasonality hypothesis (H1), predicting that timing of seasonality in mass gain and loss changes through ontogeny due to life history variation in the trade-offs toward investments in structural growth versus fat storage, reproduction, and future survival even in the same seasonal environments.

MATERIALS AND METHODS

Study area and population

The longitudinal data on red deer body mass derive from animals that were kept in the enclosure at Songli Research Station (latitude 63.343, longitude 9.649), Orkland, Norway. The enclosure covered approximately 20 ha of natural, mixed vegetation in a south-facing slope going from approximately 300 to 400 m above sea level. Winters normally last from December to April, and snow depth regularly exceeded 60–80 cm. The topography created an elevational gradient to snow melt, vegetation development, and availability in spring. The field layer was characterized by a natural variety of herbaceous plants, sedges, and grasses, depending on the dryness of the ground. Bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) species were well represented, and shrubs like juniper (*Juniperus communis*) and various willow species (*Salix* spp.) occurred especially at higher elevations. Birch (*Betula* spp.) was the dominating tree species together with smaller groups of young spruce (*Picea abies*). Some older pine trees (*Pinus silvestris*) occurred scattered in the upper parts of the enclosure. A smaller section (1 ha) in the lower part was all grassland. The vegetation within the enclosure hence mirrored vegetation typical for red deer habitats in the region.

Captive research animals and feeding

The animals were raised in the enclosure from birth. However, some (11 of 72) were born in the wild and brought to the research station as calves due to orphaning. At arrival, these calves were most likely less than 7–10 days old, considering body mass and the fact that they showed freezing response, typical for the first week of life in red deer (Espmark & Langvatn, 1985). Calves born in the wild were bottle-fed four times a day for the

first two months with a solution of 180 g high nutritious forage developed for young cattle (“Kalvegødt”) dissolved in 1 L of lukewarm water. During the following months, the number of feeding bouts as well as the amount of artificial nutrition was gradually reduced to finally cease at the end of November. Hand-reared calves were encouraged to explore natural vegetation. After a couple of months, all calves were offered a handful of oats on a daily basis to get them used to handling. Yearlings and older animals grazed exclusively on natural vegetation from approximately May to October. Later in autumn and in winter they also had access to dried hay *ad libitum*, in addition to natural forage available. Like calves, the yearlings and adults were also offered limited amounts of oats on a regular basis. An effort was made to run a similar and consistent feeding regime across years.

The data on body mass

Data on body mass were available from a total of 31 female and 43 male red deer during the years 1970–1999. We excluded one male and one female born in September. Of the 23 females and 38 males with known birthday, 84% (51) were born in June, 5% (3) in May and 11% (7) in July. The remaining 11 individuals were the wild-born ones and assumed to be born in June. Individual life span ranged

from 12 years (149 months) for males up to 20 years (247 months) for females, but individual sample size across ontogeny declined more rapidly for males than females due to culling (Appendix S1: Figure S1). When fitting the growth models, we restricted the data set to young and prime ages only (0–12 years), avoiding any effects of senescence (indicated in the data for the oldest females, Appendix S1: Figures S2 and S3).

Body mass information was obtained by getting the animals to voluntarily enter a platform scale (Figure 1). The total live body mass was estimated to the nearest 0.5 kg. Some individuals had to be teased with a handful of oats to enter the scale, and in some cases, jumpy calves had to be weighed together with the mother. The mass of the mother was then subtracted from the gross result to give the calf mass. Body masses were mainly recorded in the morning between 08:00 and 12:00 in order to reduce the daily mass variation in the measurements, which may be up to approximately 3 kg at an individual level (R. Langvatn, unpublished data). Most individuals were measured several times per year throughout their life, but some of the wild caught red deer initially were hesitant to enter the scale and had larger time intervals of no measurements at early age (Appendix S1: Figure S3). The statistical models accounted for repeated measurements through individual random effects.



FIGURE 1 A picture of an adult red deer voluntarily entering the platform scale for weighing at Songli Research Station, Norway. Photo credit: Rolf Langvatn.

Description of growth models

As a starting point, we consider the following commonly used annual growth models for mass M_t (in kilograms) at age t (in years):

1. The von Bertalanffy model:

$$M_t = W_\infty (1 - De^{-Kt})^3. \quad (1)$$

2. The Brody model:

$$M_t = W_\infty (1 - De^{-Kt}). \quad (2)$$

3. The Gompertz model:

$$M_t = W_\infty \exp(-De^{-Kt}). \quad (3)$$

Here, W_∞ represents the asymptotic size, D describes how much of the asymptotic size is to be gained after birth, and K is a growth coefficient describing the rate at which the size approaches the asymptotic size. The models are illustrated in Appendix S1: Figure S4.

To model seasonal growth, we define age in months instead of years and use sine functions to capture seasonal changes. In a first set of expansions to the baseline model, a sine function is included in the growth exponent so that the seasonal effect declines with age.

1. Seasonal von Bertalanffy model 1:

$$M_t = W_\infty \left(1 - D \exp \left[-Kt - B \sin \left(\frac{2\pi(t-s_1)}{12} \right) \right] \right)^3. \quad (4)$$

2. Seasonal Brody model 1:

$$M_t = W_\infty \left(1 - D \exp \left[-Kt - B \sin \left(\frac{2\pi(t-s_1)}{12} \right) \right] \right). \quad (5)$$

3. Seasonal Gompertz model 1:

$$M_t = W_\infty \exp \left(-De^{-Kt - B \sin \left(\frac{2\pi(t-s_1)}{12} \right)} \right). \quad (6)$$

In the seasonal component, the parameter B defines the amplitude and s_1 sets the peak month within each year. However, due to the nonlinearity of the growth model, this does not directly translate to the amplitude of the mass. The other parameters have the same definition as in the baseline models, except that age and therefore growth is now defined on a monthly scale. These models will not capture lasting fluctuations at older ages because the seasonal component will decline with age

but is included for comparison with the other seasonal models.

A second expansion to the baseline models include a seasonal component with amplitude that does not decline with age, resulting in models with fixed seasonality.

1. Seasonal von Bertalanffy model 2:

$$M_t = W_\infty (1 - D \exp[-K(t-t_0)])^3 \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (7)$$

2. Seasonal Brody model 2:

$$M_t = W_\infty (1 - D \exp[-Kt]) \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (8)$$

3. Seasonal Gompertz model 2:

$$M_t = W_\infty \exp(-De^{-Kt}) \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (9)$$

In the seasonal component of these models, the parameter C defines the amplitude and s_2 defines the phase-shift-determining peak month within each year. Other parameters have the same definitions as in the other models.

A final set of seasonal models includes both kinds of seasonal components described above, one where the effects decline over ontogeny and one that describes lasting fluctuations, resulting in models with shifting seasonality.

1. Seasonal von Bertalanffy model 3:

$$M_t = W_\infty \left(1 - D \exp \left[-K(t-t_0) + B \sin \left(\frac{2\pi(t-s_1)}{12} \right) \right] \right)^3 \times \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (10)$$

2. Seasonal Brody model 3:

$$M_t = W_\infty \left(1 - D \exp \left[-Kt - B \sin \left(\frac{2\pi(t-s_1)}{12} \right) \right] \right) \times \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (11)$$

3. Seasonal Gompertz model 3:

$$M_t = W_\infty \exp \left(-De^{-Kt - B \sin \left(\frac{2\pi(t-s_1)}{12} \right)} \right) \times \left(1 + C \sin \left(\frac{2\pi(t-s_2)}{12} \right) \right). \quad (12)$$

Statistical models

All models were fitted in R version 4.3.0 (R Development Core Team, 2023) using nonlinear mixed effects models in package nlme (Pinheiro et al., 2023). For each model defined above (Equations 1–12), we included fixed effects of sex on each parameter (W_{∞} , K , D , B , C , s_1 , and s_2 , depending on the model). Models (1)–(6) were only fitted for illustrative purposes, as they are not relevant for the red deer data, while models (7)–(12) were fitted as candidate models to be compared. Random effects of individuals were included on D and K (Appendix S1: Figures S10 and S15), and residual autocorrelation was captured by including an autoregressive process of order 1 (for models 7–12, Appendix S1: Figures S8, S9, S13, and S14). Models were compared using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). Compared with the model with lowest AIC (or BIC), we considered models with ΔAIC (or ΔBIC) ≤ 2 to have much support (being equally good), models with $4 \leq \Delta\text{AIC}$ (or ΔBIC) ≤ 7 to have considerably less support, and models with ΔAIC (or ΔBIC) > 10 to have essentially no support, following the rules of thumb outlined by Burnham and Anderson (2004). The 95% CIs for the predicted growth curves were calculated based on 1000 bootstrap samples of the estimated fixed effect coefficients, using a multivariate normal distribution based on the estimated variance–covariance matrix. The R code for fitting the different growth models is provided in Appendix S1 and in Zenodo (Vindenes et al., 2023), where additional plots of models and residuals are shown. We also refitted the best supported model to the dataset for females only to check that we get approximately the same result as for the female part from the model fitted to both sexes (Appendix S1: Figure S17).

Finally, we tested the effects of our assumption that all individuals were born in June. This assumption means the translation of age to month within year will be offset by one month for those born in July or May. Most individuals were born in June (see above *The data on body mass*).

We refitted the best supported model to another dataset using “June-relative ages,” where those born in July were assigned “June-relative age = -1 ” for each month relative to those born in June, whereas those born in May were assigned “June-relative age = $+1$ ” relative to individuals born in June. This approach gave almost the same result (Appendix S1: Figure S18).

RESULTS

A comparison of the candidate growth models with fixed (H0) versus shifting seasonality across ontogeny (H1) showed strong support for the model with shifting seasonality for each baseline model considered (Table 1). The fitted growth curves for each fixed (Equations 7–9) and shifting seasonality (Equations 10–12) model are shown in Figure 2, while results for the fitted annual baseline models (Equations 1–3) and seasonal models with damped fluctuations (Equations 4–6) are shown in Appendix S1: Figures S5 and S6. Overall, the Brody model with shifting seasonality (Equation 11) was the best supported of all models and the Brody model with a fixed seasonal component (Equation 9) was the second best supported, indicating that this model outperforms the von Bertalanffy model and the Gompertz model regardless of whether seasonality is fixed or shifting.

The best fitting seasonal Brody model (Equation 11) allows the annual peak to shift with age (Figures 2 and 3). The estimated fixed effects coefficients for this model are shown in Table 2 and extracted parameters for males and females in Table 3. All parameters are significantly different for males and females, but the main difference among sexes is in the overall size and magnitude of the fluctuations (males being larger at older age, with larger seasonal fluctuations), not in the timing of seasonality. Adults of both sexes show a maximum size around September each year, while calves continue to grow for longer during the fall and show a peak around December (Figure 3). Yearlings show a maximum around November, while

TABLE 1 Comparison of the growth models with fixed and shifting seasonality, for male and female red deer in Norway.

Baseline model	Seasonality	df	AIC	BIC	ΔAIC	ΔBIC	Rank
von Bertalanffy	Fixed (7)	15	23,747	23,842	82	57	2
von Bertalanffy	Shifting (10)	15	23,665	23,785	0	0	1
Brody	Fixed (8)	15	23,655	23,750	122	97	2
Brody	Shifting (11)	19	23,533	23,653	0	0	1
Gompertz	Fixed (9)	15	23,749	23,843	88	62	2
Gompertz	Shifting (12)	19	23,661	23,781	0	0	1

Note: Numbers in parentheses are equation numbers. For each baseline model, ΔAIC and ΔBIC show the difference in AIC and BIC, respectively, compared with the best supported model. See *Materials and methods* for detailed description of the models.

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion.

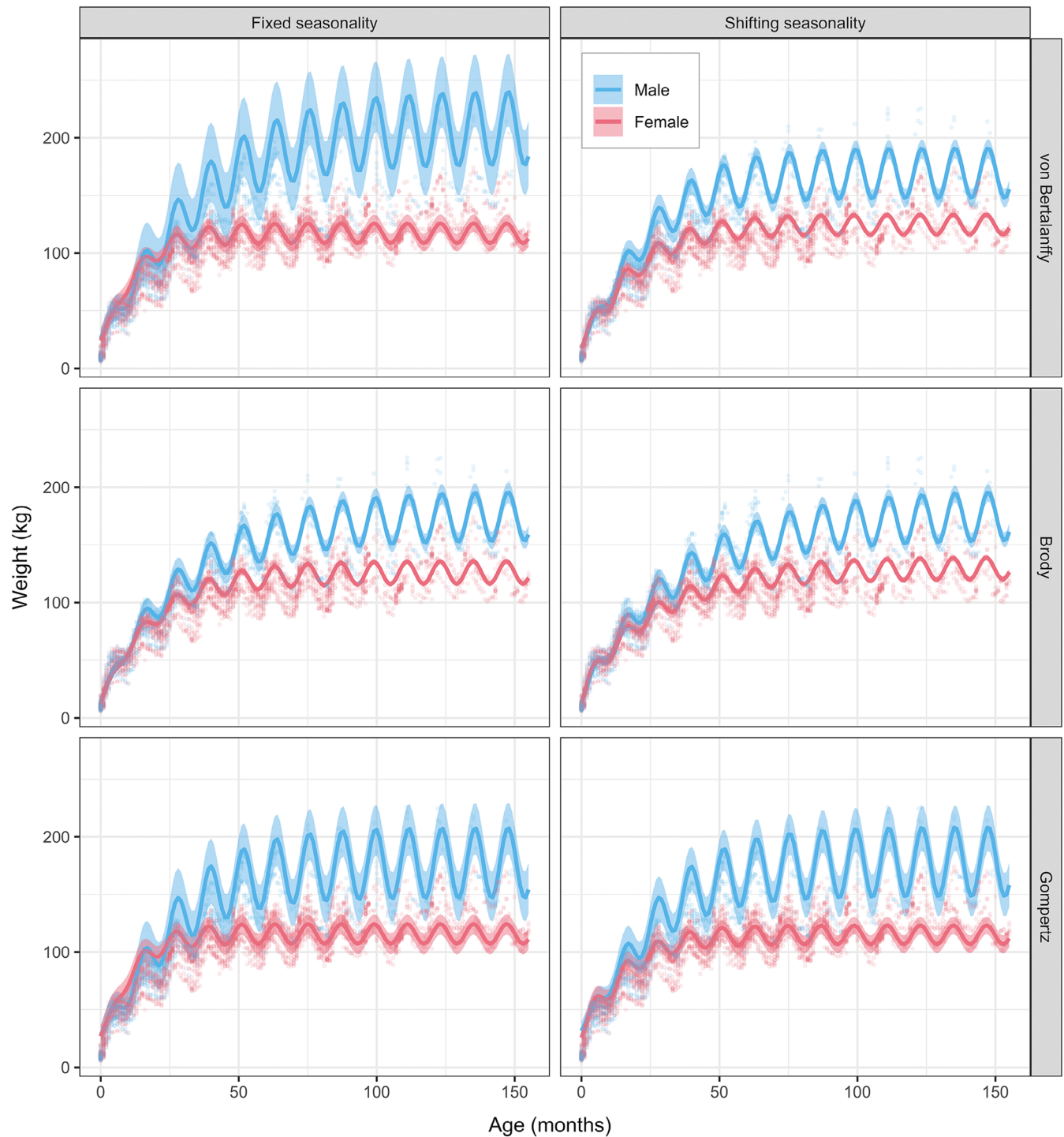


FIGURE 2 Fitted seasonal growth models for male and female red deer, with either fixed or shifting seasonality with different baseline growth models (von Bertalanffy, Brody, and Gompertz). The shifting seasonality models include two seasonal components allowing the annual peak to shift through ontogeny, while the fixed seasonality models have only one component and the same peak each year. For each growth curve the first peak represents the calves, the second peak yearlings, etc. The shading represents 95% CIs obtained from parametric bootstrapping (1000 samples).

2- and 3-year-old subadults peak around October, closer to the peak for adults (Figure 3). All age classes show a seasonal minimum at the end of winter in March. The amplitude of seasonal minimum and maximum increases throughout the entire ontogeny (Figures 2 and 3).

DISCUSSION

Even though the “old knowledge” that ungulates show marked seasonal fluctuations in body mass (Mautz, 1978; Mitchell et al., 1976; Moen, 1978), there is surprisingly no

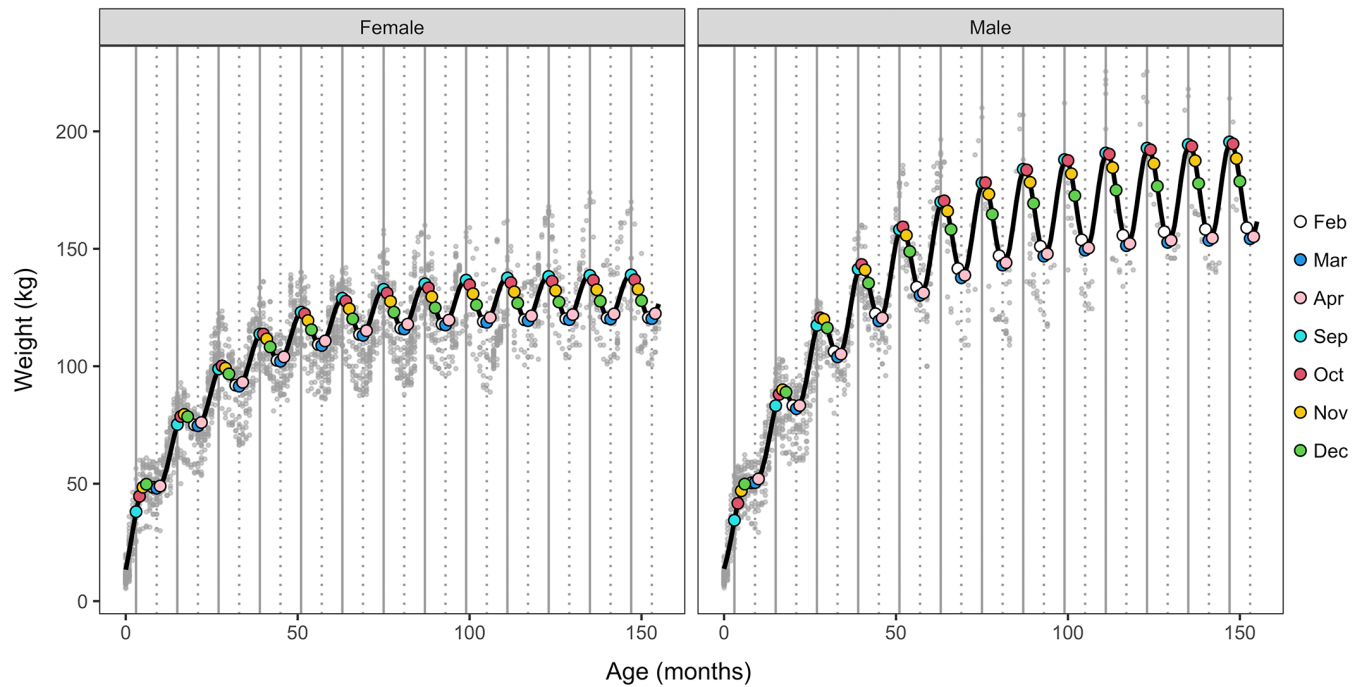


FIGURE 3 Predicted growth of red deer females and males through the first 155 months according to the seasonal Brody model 3 (Equation 11), the model with most support. Specific months are highlighted using colored points (see key). The vertical lines indicate September (solid lines) and March (dotted lines).

TABLE 2 Estimated fixed effects in the best supported model (seasonal Brody model 3, Equation 11).

Effect	Value	SE	df	<i>t</i>	<i>p</i>
$W_{\infty,0}$	176.942	3.897	3951	45.400	0.000
$W_{\infty,F}$	-46.984	4.107	3951	-11.439	0.000
K_0	0.030	0.003	3951	11.667	0.000
K_F	0.009	0.004	3951	2.290	0.022
D_0	0.892	0.009	3951	98.504	0.000
D_F	-0.062	0.016	3951	-3.921	0.000
C_0	-0.121	0.005	3951	-25.192	0.000
C_F	0.195	0.006	3951	33.152	0.000
B_0	0.034	0.006	3951	5.497	0.000
B_F	-0.115	0.010	3951	-11.061	0.000
$s_{2,0}$	18.341	0.082	3951	222.949	0.000
$s_{2,F}$	5.298	0.116	3951	45.672	0.000
$s_{1,0}$	15.672	0.312	3951	50.291	0.000
$s_{1,F}$	-7.153	0.373	3951	-19.164	0.000

Note: Parameters with subscript 0 refer to intercept values representing males. Subscript F refers to female effects that, when added to the intercept, give the corresponding parameter value for females (Table 3). Estimated individual random effect SDs are $\sigma_D \approx 0.028$ and $\sigma_K \approx 0.012$, with correlation 0.969. Estimated lag-1 autocorrelation is $\varphi \approx 0.874$. Residual SD is $\sigma_R \approx 8.859$.

detailed model that can capture shifts both in timing and amplitude of seasonal growth through ontogeny. Changes in body mass in early ages largely reflect

changes in structural mass (skeletal growth), while for adults, the annual fluctuations reflect mainly changes in reserves (fat and to some extent muscles). Our best supported model shows that the peak body mass shifts from December in calves to September in adults (from age 3 and older; Figure 3). This complex pattern likely results from ontogenetic differences in behavior, physiology, and trade-offs in energy allocation (Parker et al., 2009). Compared with earlier models of seasonal growth (Leader-Williams & Ricketts, 1982; Moen, 1978; Suzuki et al., 2001), we provide a more flexible model that captures the shift in the timing of the annual peak through ontogeny.

The annual body mass cycles of red deer varied as predicted through ontogeny (Figure 3). Young individuals grew longer into the fall than prime-age adults. Primiparous female red deer (age 1–2) have a delayed onset of rut compared with prime-aged females (Langvatn et al., 2004), and along with calves may prioritize feeding for a longer time period, while prime-aged females can prioritize getting a head start of the next years breeding cycle. We had a limited sample of older males, but reported patterns of extended growth in males are consistent with analysis of transversal data on body mass of red deer in Norway (Myrsterud et al., 2001). Males continue structural growth of body size well into adulthood, while the loss of stored reserves is age-dependent and increases during the rutting season in fall

TABLE 3 Estimated mean parameter values for females and males in the best supported growth model (seasonal Brody model 3, Equation 11), from the estimated fixed effects (Table 2).

Sex	W_{∞}	K	D	C	B	s_2	s_1
Female	129.958	0.038	0.830	0.074	-0.081	23.640	8.519
Male	176.942	0.030	0.892	-0.121	0.034	18.341	15.672

(Myerud et al., 2004; Yoccoz et al., 2002). This is a general and well-known pattern of many polygynous mammals. In bears, females also cease structural growth at an earlier age than males, as shown in black bears (*Ursus americanus*) (Bartreau, 2019), brown bears (*Ursus arctos*) (Kingsley et al., 1988), and polar bears (*Ursus maritimus*) (Derocher & Wiig, 2002). This growth pattern leads to more marked sexual body-size dimorphism with increasing age (Festa-Bianchet et al., 1996). In our best fitting model, growth peaked at approximately the same time in fall for both sexes, but as expected, males grew to larger sizes and adult males show larger intra-annual fluctuations.

The lack of sufficiently detailed seasonal growth models described in the literature is probably in part driven by a lack of data required to fit such models. It is exceedingly difficult to obtain detailed longitudinal seasonal data on body size from wild populations. We here benefitted from data of captive red deer in a large enclosure with a stable winter-feeding regime. The seasonal fluctuations in body mass in the wild result from a combination of changes in forage intake (Weber & Thompson, 1998), activity levels (Cederlund, 1981), and metabolism (Arnold et al., 2004; Moen, 1978). Wild red deer move less during winter (Pépin et al., 2009), and their home range size is more restricted (Rivrud et al., 2010), but this is clearly different from captive deer living in an enclosure. In black-tailed deer, seasonal changes in body mass of wild deer were greater than those for captive deer of the same age (Parker et al., 1993), and this may well be the case also for red deer so that our results represent a conservative estimate of annual fluctuations of body size in the wild. Another study found that metabolism was reduced with 60% in captive red deer during winter (Arnold et al., 2004), and female reindeer showed seasonal reduction in forage intake despite having access (Tyler et al., 1999). These seasonal physiological rhythms are key to explain the regular body mass declines observed during winter in this study, despite the deer having access to forage in captivity.

Variation in timing of birth is a challenge when fitting seasonal growth models over the ontogeny, as it creates a link between age and date on body mass of calves at a given date in fall (Holand et al., 2006). Timing of birth is typically highly synchronized at northern latitudes (Fletcher, 1974; Rutberg, 1987), and the birth

period covered a little over a month in the captive red deer population in Norway (Loe et al., 2005). Our alternative model where ages were adjusted relative to June (“June-relative age”) gave practically the same results as the model without adjusted ages with minimal effects on the growth curve (Appendix S1: Figure S18). The effects may be larger for species where births are less synchronized than red deer. Thus, the presented growth model is best suited to species with synchronous birth but can be adjusted to account for different timing of birth. At the other end of life, ungulates show senescence in survival, reproduction, and body mass (Gaillard et al., 2004). Red deer have onset of senescence in body mass at ~20 years of age for females (Myerud et al., 2001) and 8–10 years for males (Yoccoz et al., 2002), which is much later than for survival and reproduction (Langvatn et al., 2004). Due to the limited data at old ages and signs of senescence in these few individuals, we removed data points over 156 months (age 13). We can predict a lower amplitude and later timing of annual peak in body mass after the onset of senescence (Langvatn et al., 2004), which would require further model sophistication and a larger data set for old ages.

We used sine functions to capture the seasonal growth dynamics, and in the most complex shifting models, we incorporated two seasonal components that would allow the peak to shift with age as well as the fluctuations to approach a stable cycle over time. Using trigonometric functions to describe seasonality is common for a range of systems, and growth models incorporating sine functions leading to damped fluctuations have previously been developed for fish (Pauly et al., 1992; Pitcher & Macdonald, 1973). When the goal is to capture differences in growth rate over season within a length-based model where individuals do not shrink, it is reasonable to assume damped fluctuations. But for mass-based growth models where individuals continue their seasonal mass fluctuations also as adults, the seasonal growth model should allow for persisting cycles. Here we presented a model that allows the seasonality (location of peak) to shift with age as well as approach a persisting cycle for adults, which is more flexible than previous models. The sine function represents an approximation of actual seasonal changes in mass, and the red deer data suggest that the annual peaks are sharper than in a sine function,

with more gradual increase and decline in the latter. In the statistical models, we capture residual autocorrelation due to this difference using a correlation function. An alternative approach to describe seasonal growth with shifts through ontogeny would be to define more mechanistic models based on energy intake and expenditure and specifically model ontogenetic changes in allocation of energy to growth, reproduction, and survival (maintenance). Such an approach would require more detailed data on physiology and metabolism, as well as data on energy intake rates. Our current model does not include any physiological mechanisms and is based on mass-data alone yet is able to capture the main patterns of seasonality. Its main purpose is to identify changes in seasonality over ontogeny, whereas identifying the exact mechanisms behind these changes will require more detailed mechanistic growth models.

Our flexible seasonal growth model allowed estimation of different amplitude and timing of annual peaks depending on age, reflecting age-dependent trade-offs connected to growth in structural size versus condition, reproduction, and survival. High-quality growth models are also a key part of structured population dynamics models, such as integral projection models, where body size is linked to survival and reproduction, and growth ultimately affects fitness and population growth patterns. Our growth model can also be extended to include effects of environmental variables or other external drivers affecting the model parameters, based on the nonlinear mixed effects modeling approach. Incorporating this with population dynamics models can provide a useful tool to understand and project the population dynamics impacts of changes in land use, related to agriculture (Mysterud et al., 2022), and in summer and winter (Rivrud et al., 2019).

AUTHOR CONTRIBUTIONS

Atle Mysterud drafted the first version of introduction and discussion, Rolf Langvatn wrote parts of study area and animal handling, while Yngvild Vindenes wrote methods and results. Yngvild Vindenes defined the growth models, did the statistical modeling, and wrote the Appendix. Rolf Langvatn provided the data. All the authors contributed to further drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.


DATA AVAILABILITY STATEMENT

Data and code (Vindenes et al., 2023) are available from Zenodo: <http://doi.org/10.5281/zenodo.7499267>.

ETHICS STATEMENT

The facilities were approved for keeping animals by the ethical board of research in Norway (“Forsøksdyrutvalget”).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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