Animal (2020), **14:S1,** pp s124–s132 © The Animal Consortium 2020
doi:10.1017/S1751731119003240

animal

Review: Seasonal differences in the physiology of wild northern ruminants

W. Arnold†

Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Savoyenstraße 1, Vienna A-1160, Austria

(Received 20 May 2019; Accepted 21 August 2019)

Ruminants living in seasonal environments face a two-fold challenge during winter. The energetic cost of maintaining a high body temperature is higher at lower ambient temperatures, and this is compounded by poor availability and quality of feed. Wild ruminants acclimatize to this energetic challenge by hypothermia, that is, reduced endogenous heat production and abandoning the maintenance of a high body temperature, particularly in peripheral body parts. Further but lesser contributions to lower energy expenditure during winter are reduced foraging activity; lower heat increment of feeding; and reduced maintenance cost of size-reduced organs. Altogether, metabolic rate, estimated by the continuous measurement of heart rate, during winter is downregulated to more than half of the summer level, as is voluntary food intake, even in animals fed ad libitum*. The transformation from the summer into the thrifty winter phenotype is also evident in the physiology of digestion. Microbial protein synthesis is less facilitated by diminished phosphorus secretion into the shrunk rumen during winter. In line with this result, the concentration of ammonia, the end-product of protein digestion in the rumen, peaks in rumen liquid in spring, whereas the molar proportion of acetate, an indicator of fermentation of a diet rich in fiber, peaks in winter. In contrast to reduced stimulation of growth of ruminal microbes during winter, active transport of nutrients across the intestinal epithelium is increased, resulting in more efficient exploitation of the lower amount and quality of ingested winter feed. Nevertheless, the energy balance remains negative during winter. This is compensated by using fat reserves accumulated during summer, which become a major metabolic fuel during winter.*

Keywords: seasonal acclimatization, metabolic rate, thermoregulation, digestion, organ size

Implications

The dramatic change of environmental conditions among seasons is a challenge for free-living animals. Wild northern ruminants acclimatize to seasonality by adjusting both physiology and behavior. A profound decrease of energy expenditure during winter, mostly achieved by a decrease in body temperature, allows a decline in voluntary feed intake. However, digestion of ingested feed becomes simultaneously more efficient. Similar reactions may also be present in domesticated ruminants, at least in primordial breeds. A better understanding of the mechanisms and extent of seasonal acclimatization will help to improve both animal keeping and wildlife management.

Introduction

High latitudes and altitudes are characterized by profound differences in environmental conditions between summer and winter, particularly for herbivores. Outside the vegetation period, the availability and quality of plant material is considerably lower, and feed is difficult to access if covered by snow. In addition, temperatures are much lower during winter, causing endothermic organisms to expend more energy for thermoregulation. Many small mammals cope with these difficulties by entering hibernation or daily torpor (Geiser and Ruf, 1995). Among large mammals, such reactions were for a long time only known from bears. Non-hibernating large mammals under cold load seemed to minimize energy requirements solely by changing to a well-insulating winter fur, counter-current heat exchange mechanisms and reduced locomotor activity. With the advance of telemetry techniques, it became possible to measure physiological and behavioral reactions in free-living animals continuously over long periods. These data unequivocally answered the long-standing question of whether seasonal changes of metabolic rate in northern ungulates are predominantly due to different intake of feed (and hence heat increment of feeding), or to changes of endogenous heat production (and thus basal metabolic rate), similar to the reactions of

† E-mail: walter.arnold@vetmeduni.ac.at

hibernators and daily heterotherms (Arnold et al., 2004, 2006; Turbill *et al.*, 2011).

In this paper, I review studies addressing the question of seasonal acclimatization of physiology and energy expenditure of northern wild ruminants. I further present as-yet-unpublished data and analyses of samples delivered by hunters to the Research Institute of Wildlife Ecology during the years 1970 to 2006.

Metabolism and body temperature regulation

In all wild northern ruminant species where seasonal acclimatization has been studied in appropriate detail (i.e. with long-time measurements of high resolution), profound changes have been found during the year in physiological and behavioral parameters (Figure 1). Although these species do not hibernate or show daily torpor in the classical sense, they do become hypometabolic during the winter, as indicated by a reduction of heart rate (f_H), a good proxy of metabolic rate (Turbill *et al.*, 2011). This reduction is most pronounced in species dwelling in alpine (chamois, Alpine ibex) or polar habitats (Svalbard reindeer) with particularly harsh winter conditions (Figure 1).

The reduction of energy expenditure during winter is accomplished to some degree by reduced locomotor activity reflecting less foraging (Arnold *et al.*, 2018), but most strongly correlates with body temperature (T_b) measured in the rumen (T_r, slightly higher but closely following core T_b; Beatty *et al.*, 2008) (Figure 1). Decreased endogenous heat production as the major contribution to reduced metabolic rate during winter has been found in many species of ungulates (Arnold et al., 2004, 2006; Signer *et al.*, 2011; Turbill *et al.*, 2011; Brinkmann *et al.*, 2012; Riek *et al.*, 2017; Arnold *et al.*, 2018). In red deer, for instance, the annual variation of T_r is in the range of 0.5°C, which is sufficient to explain most of the annual variation of f_H (estimated effect size 24.5 beats/min, annual range of f_H variation 30 beats/min; Turbill *et al.*, 2011). The effect is greater than expected from the Newtonian equation of thermoregulatory heat production. The discrepancy was initially postulated to be the result of the simplified calculation assuming a uniform temperature throughout the body. However, red deer – and presumably all wild ungulates living in seasonally cold environments – allow substantial peripheral cooling, particularly during nocturnal bouts of hypometabolism, with subcutaneous temperature measured at the neck dropping to 15°C during late winter nights (Arnold *et al.*, 2004). Therefore, a slightly lower core T_b apparently indicates a much greater reduction in the mean temperature of the entire body mass and hence basal metabolic rate. Allowing considerably low temperature in peripheral parts of the body, particularly in the extremities, has long been known as an important thermoregulatory strategy in mammals and birds of the Arctic (Irving and Krog, 1955). The evidence available now challenges the traditional view that a change in thermal conductance is the primary mechanism available to large mammals for reducing their thermoregulatory energy expenditure (Scholander *et al.*, 1950). Instead, large mammals seem to reduce endogenous heat production in response to cold exposure and nutritional bottlenecks (Turbill *et al.*, 2011; Brinkmann *et al.*, 2017; Thompson *et al.*, 2019). This process is analogous to that of small species employing daily torpor or hibernation and has, at least temporally, comparable consequences for T_b in peripheral parts of the body (Arnold et al., 2004, 2006; Brinkmann *et al.*, 2012). Experimental food restriction elicits a further decrease of f_H and T_r during winter (Turbill *et al.*, 2011; Brinkmann *et al.*, 2017), but does not suppress the pronounced increase of f_H and T_r in spring, nor does *ad libitum* feeding prevent the decline toward the winter trough (Turbill *et al.*, 2011).

Use of fat reserves

Another analogy to hibernation, manifest in wild northern ungulates, is the switch to body fat reserves as an important metabolic fuel. These fat reserves are built up during summer and autumn and are consumed during winter (Figure 2). The use of body fat reserves during winter is apparently associated with a reduction of appetite and hence less motivation to search for scarce winter feed. Red deer, for instance, halve their feed intake during winter even when fed *ad libitum* (Arnold *et al.*, 2015b). The seasonal difference in energy intake is similar to that caused by reproduction during peak lactation in June (Figure 3). The reduction of appetite during winter is controlled by photoperiod (Loudon, 1994) and seems to be ubiquitous among wild northern ungulates (Peltier *et al.*, 2003; Arnold *et al.*, 2004; Barboza *et al.*, 2006; Kuntz *et al.*, 2006; Crater and Barboza, 2007; Brinkmann *et al.*, 2017). Changes in feed intake, on the other hand, lead to a different heat increment of feeding, which contributes to seasonal changes of metabolic rate, although not close to the extent as previously thought (Lawler and White, 2003; Arnold et al., 2004, 2006; Turbill *et al.*, 2011).

Organ size and body mass

Since less feed needs to be processed during winter, this can be accomplished with a smaller alimentary tract, which additionally saves energy necessary for maintaining expensive tissue (Stevens and Hume, 1995). Profound shrinking of the gut and visceral organs, for instance, occurs in marmots during hibernation (Hume *et al.*, 2002), but is also known from chamois, red deer and roe deer, and takes place even when animals are fed *ad libitum* (Arnold *et al.*, 2015b). Data on liver mass, available from free-living animals of three species of wild ruminants, clearly demonstrate the magnitude of seasonal change in the size of visceral organs (Figure 4). Due to changes in fat reserves and organ size, total body mass also shows a considerable seasonal variation (Figure 5; similar changes are reported for Alpine ibex (Giacometti *et al.*, 1997), bighorn sheep (Pelletier *et al.*, 2011),

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

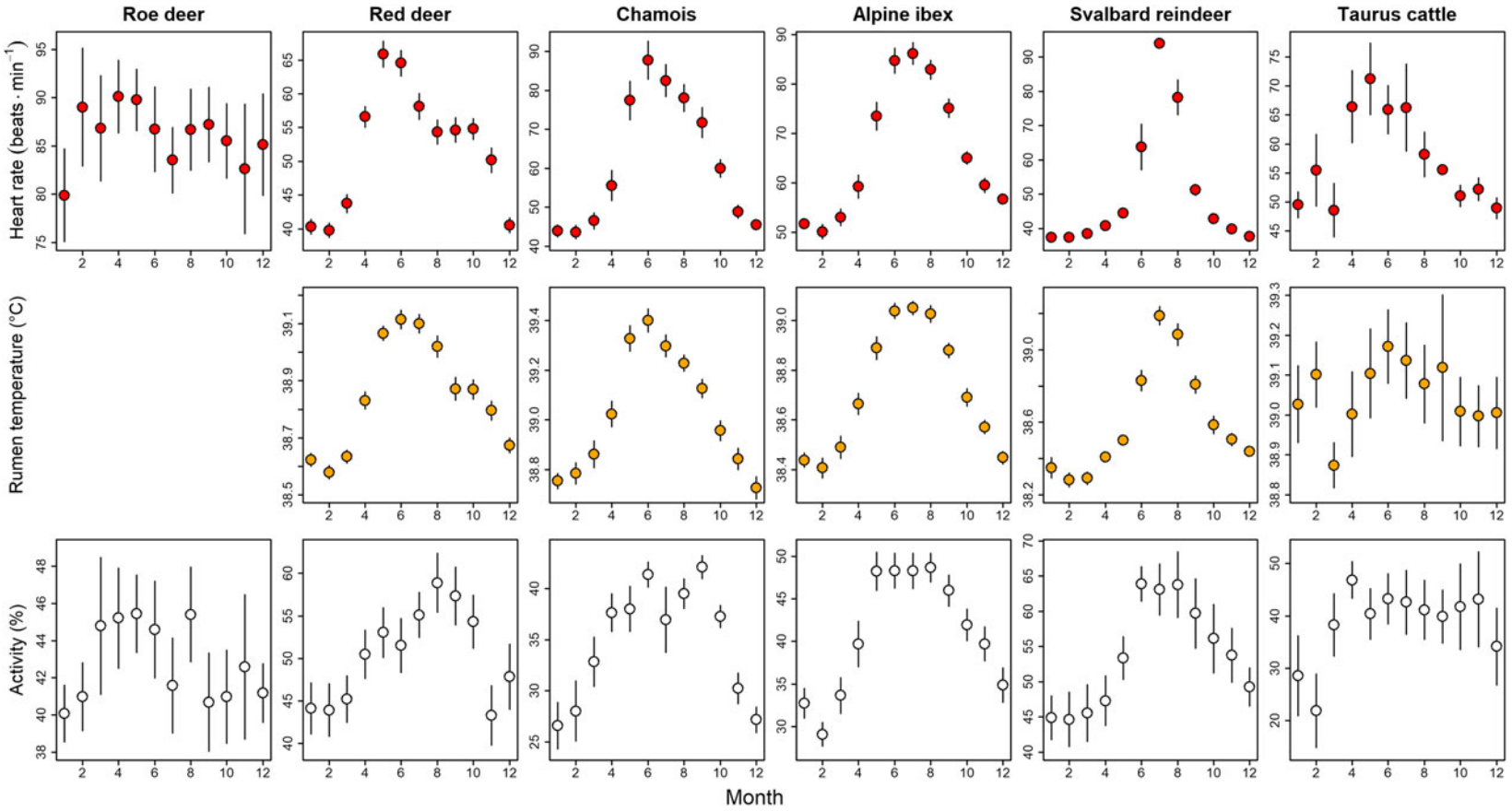

Figure 1 (colour online) Seasonal change of heart rate, rumen temperature and activity in six species of wild ungulates (roe deer (*Capreolus capreolus*): re-analyzed data from Reimoser, 2012; red deer (*Cervus elaphus*): re-analyzed data from Turbill *et al.*, 2011; chamois (*Rupicapra rupicapra*): unpublished data sampled between 2009 and 2012 from nine male and seven female chamois (ages 4 to 12 years), living free in an alpine area in Upper Austria; Alpine ibex (*Capra ibex*): re-analyzed data from Signer *et al.*, 2011; Svalbard reindeer (*Rangifer tarandus platyrhynchus*): re-analyzed data from Arnold *et al.*, 2018; Taurus cattle: unpublished data from 6- to over 2-year-old females living free in Hortobágy National Park, Hungary). Taurus cattle are the result of a long quest to resurrect the extinct aurochs (*Bos primigenius*) (Stokstad, 2015). Chamois and Taurus cattle were studied with the same telemetry technique used for red deer, alpine ibex and Svalbard reindeer. Plotted are monthly means with 95% CI reflecting variation between individuals.

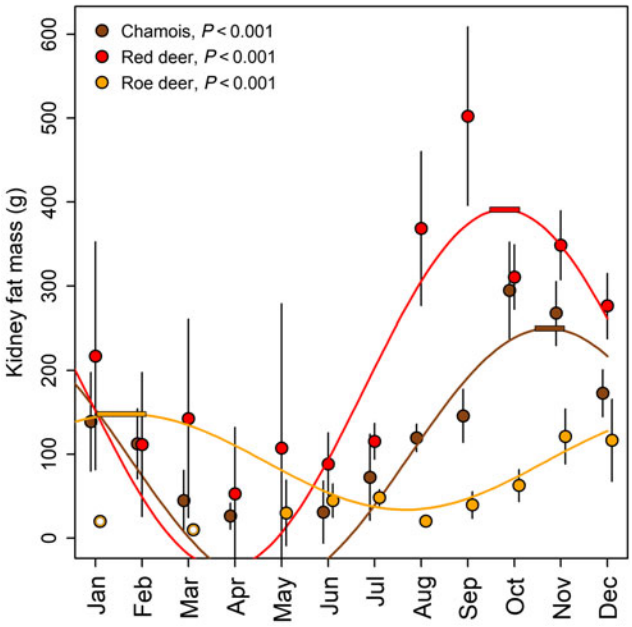

Figure 2 (colour online) Seasonal changes of kidney fat mass as an indicator of body fat reserves of free-living chamois, red deer and roe deer. Plotted are monthly means with 95% CI; single values are indicated by a white dot. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as month in radians. Lines represent periodic fits to the data; horizontal bars at peaks represents 95% CI of peak location.

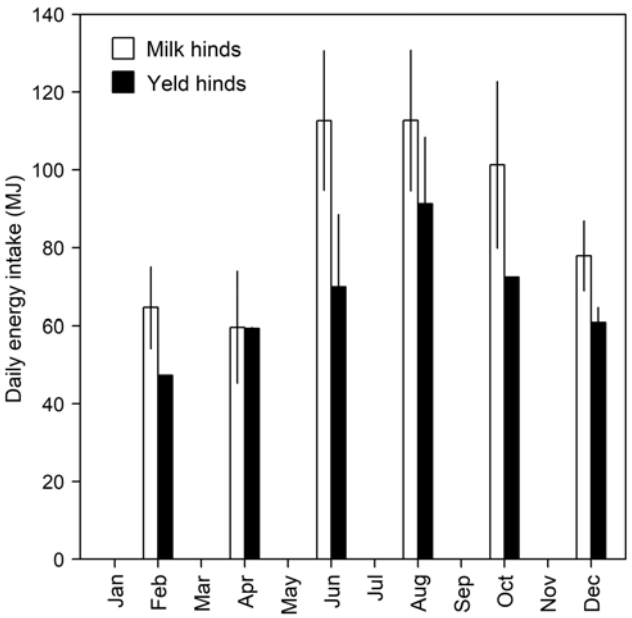

Figure 3 Seasonal changes of daily energy intake from pellets and natural vegetation of adult red deer hinds provided *ad libitum* with pellets (re-analyzed data from Arnold *et al.*, 2015b). Plotted are monthly means with 95% CI; error bars are lacking for yeld hinds in February and October because only one individual was measured; linear mixed-effects modeling: effect of month, $F_{(5,60)} = 9.53$, $P < 0.0001$; effect of reproduction, $F_{(1,60)} = 0.36$, $P = 0.552$; interaction of month and reproduction, $F_{(5,60)} = 0.44$, $P = 0.817$.

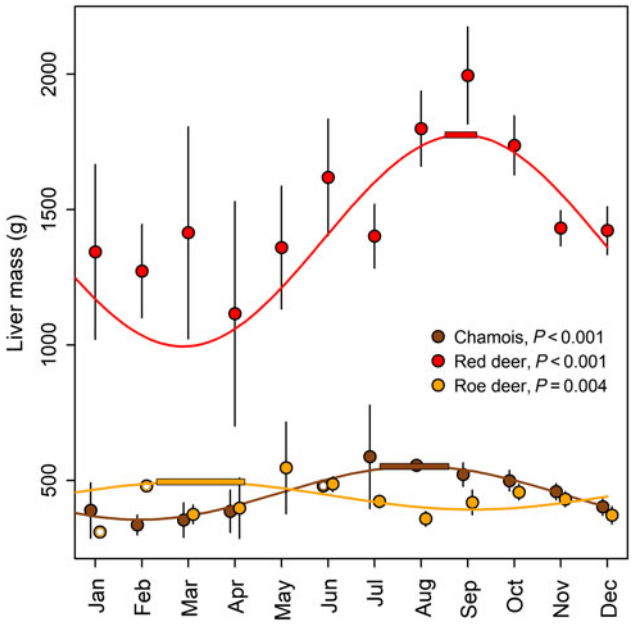

Figure 4 (colour online) Seasonal changes of liver mass of free-living chamois, red deer and roe deer. Plotted are monthly means with 95% CI; single values are indicated by a white dot. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as month in radians. Lines represent periodic fits to the data; horizontal bars at peaks represent 95% CI of peak location.

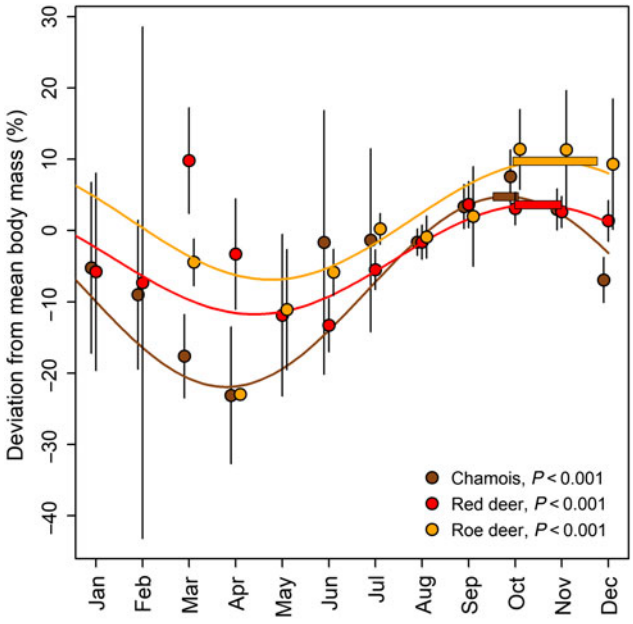

Figure 5 (colour online) Seasonal changes of body mass of free-living chamois, red deer and roe deer. Body mass is plotted as a percentage of mean body mass of the respective age/sex class of a species. Adult body mass is achieved at the age of 2 in female and 5 in male chamois, 4 in female and 7 in male red deer, 2 in female and 4 in male roe deer. Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as month in radians. Lines represent periodic fits to the data; horizontal bars at peaks represent 95% CI of peak location.

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

bison (Rutley and Hudson, 2000), black-tailed deer (Parker *et al.*, 1993), moose (Milner *et al.*, 2012), muskoxen (Crater and Barboza, 2007), reindeer (Tyler and Blix, 1990) and white-tailed deer (DelGiudice *et al.*, 1992)).

Digestion and uptake of nutrients

In contrast to the reduction of the size of alimentary tract and the surface area for nutrient absorption, the efficacy of nutrient extraction may be increased (Ferraris and Carey, 2000), as found for protein digestion in wintering red deer (Arnold *et al.*, 2015b). Three mechanisms may explain this result. Firstly, models predict that optimal digestion time is longer if food quality is low. When plants contain a high amount of lignified cell walls, the rumen-reticulum fills with residues that ferment so slowly that passage out of the forestomach is impeded (Hume, 1989). Indeed, longer retention time during periods when feed is of low digestibility seems to be common among ungulates (Lechner-Doll *et al.*, 1991; Holand, 1994; Kuntz *et al.*, 2006). However, in small ruminants such as roe deer, the strategy of increasing cell wall digestion by increased rumen retention is severely limited by the small size of the rumen-reticulum. Therefore, roe deer depend more on a selective feeding strategy to enhance winter survival than other wild ruminants (Holand, 1994).

Secondly, the expression of transporter proteins seems to be increased during winter. For example, in red deer, the uptake of dipeptides into brush-border membrane vesicles, prepared from enterocytes, is higher during winter (Arnold *et al.*, 2015b). This might be linked to seasonal expression profiles of the proton-dependent peptide transporter 1 (**pepT1**). The upregulation of pepT1 during winter could be the mechanism responsible for increased extraction of peptides from digested proteins and be an integrative part of the winter phenotype of wild ruminants. A similar scenario is likely to exist in red deer for glucose uptake (Arnold *et al.*, 2015b). Therefore, it seems that the energetic cost of additional transporter expression during winter is lower than the benefit derived from attenuating an inevitably negative energy balance by maximal exploitation of poor feed.

Thirdly, a reduction of the number and size of ruminal papillae and a smaller rumen volume, as is typical for winter-acclimatized wild ruminants (reviewed in Arnold *et al.*, 2015b), may sustain the rate of absorption of short-chain fatty acids (**SCFA**). Due to lower intake of feed, and presumably diminished microbial fermentation at lower T_r (Crater and Barboza, 2007), SCFA production is lower during winter (Figure 6; Tataruch and Onderscheka, 1993; Crater *et al.*, 2007). The uptake of SCFA, the most important source of energy for ruminants, occurs mainly by diffusion (Aschenbach *et al.*, 2011). Hence, the surface area for SCFA absorption must be reduced during winter to maintain a sufficient gradient of SCFA concentrations between rumen content and blood. Therefore, the rapid loss of mucosal mass

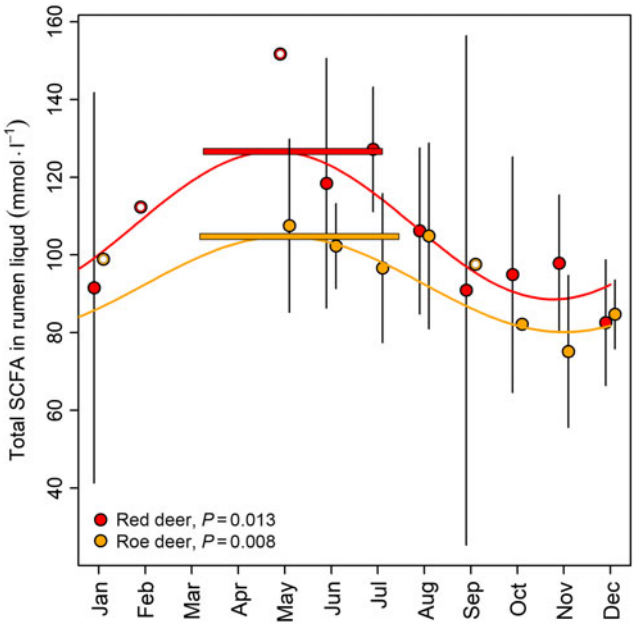

Figure 6 (colour online) Seasonal changes of total short-chain fatty acid (SCFA) concentrations in the rumen liquid of free-living red and roe deer (for methods, see Tataruch and Onderscheka, 1993). Plotted are monthly means with 95% CI; single values are indicated by a white dot. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as day of the year in radians. Lines represent periodic fits to the data; horizontal bars at peaks represent 95% CI of peak location.

induced by malnutrition might, for wild ruminants, in fact be functional. This interpretation is supported by the finding of a reduction of rumen volume by about one-third during winter in red deer, although the study animals did not lose body mass due to the availability of pellets *ad libitum* (Arnold *et al.*, 2015b). Interestingly, high SCFA concentrations, and particularly those of butyric and propionic acid, stimulate ruminal blood flow and induce the formation of new papillae by increasing the mitotic rate of papillary epithelium (Hofmann, 1989). Short-chain fatty acid concentrations in the rumen peak in spring in red deer, roe deer and chamois (Figure 6; Tataruch and Onderscheka, 1993), and at least in red deer the molar proportions of n-butyric, propionic and n-valeric acid (Figure 7; Tataruch and Onderscheka, 1993). Similar changes have been reported for mule deer (Short *et al.*, 1966) and muskoxen (Crater *et al.*, 2007). On the other hand, the molar proportion of acetate, an indicator of fermentation of a diet rich in fiber (Weiss *et al.*, 2017), is highest during winter (Figure 7; Short *et al.*, 1966; Tataruch and Onderscheka, 1993; Crater *et al.*, 2007). Higher concentrations of SCFA are indicative of high digestibility of feed, and molar proportions of n-butyric and n-valeric acid increase with the content of crude protein (**CP**) in the diet (Tataruch and Onderscheka, 1993). Further, the concentration of ammonia, the end-product of protein digestion in the rumen, also peaks in rumen liquid in spring (red deer, $P < 0.001$; roe deer, $P < 0.001$; 95% confidence interval (**CI**) of peak location: red deer, mid-April to mid-May; roe deer, early March to early May). Altogether, the changes of concentrations of fermentation products in the rumen liquid reflect the

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

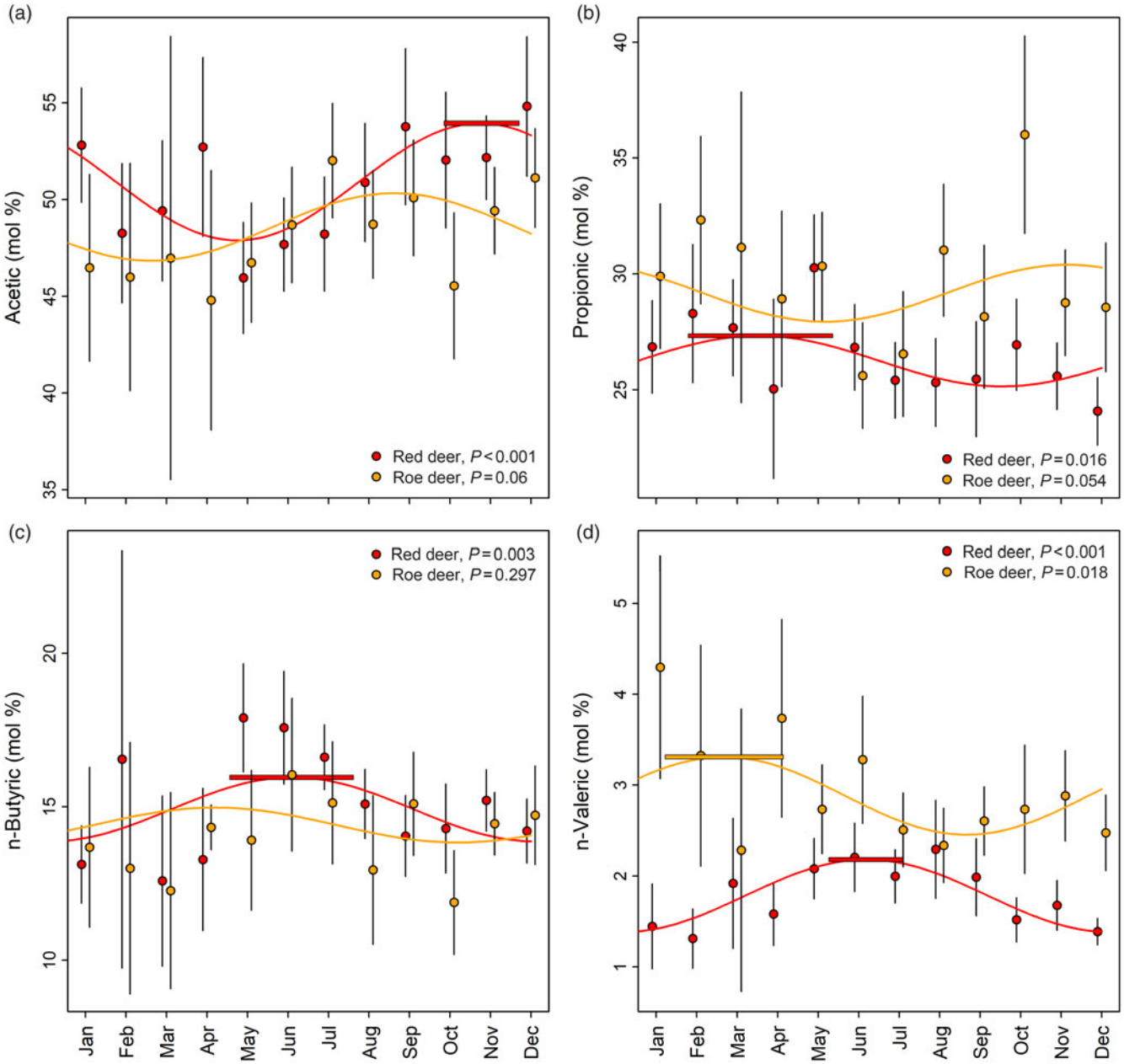

Figure 7 (colour online) Seasonal changes of the molar proportions of acetic (a), propionic (b), n-butyric (c) and n-valeric acid (d) in the total amount of short-chain fatty acids in the rumen liquid of free-living red and roe deer (for methods, see Tataruch and Onderscheka, 1993). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as day of the year in radians. Lines represent periodic fits to the data; horizontal bars at peaks represent 95% CI of peak location.

increase of feed availability and quality in spring. This may well be a signal that, together with increasing day-length, elicits the change into the anabolic summer phenotype with high metabolic rate (Figure 1) and regrowth of the alimentary tract and visceral organs (Figure 4; Arnold *et al.*, 2015b).

Stimulation of microbial protein biosynthesis by phosphorus secretion

However, seasonally varying feed quality and T_r are not the only variables that shape the community of ruminal symbionts. A further mechanism seems to be seasonally changing concentrations of phosphorus in the rumen content (Figure 8). The CI of location of peak phosphorus concentration overlaps in each species with the CI of location of peak concentration of CP in the rumen content (cf. Figures 8 and 9). Phosphorus is essential for the growth and protein synthesis of ruminal microbiota (Durand and Kawashima, 1980). High phosphorus concentrations during summer indicate increased delivery by the host, presumably via saliva (Breves and Schröder, 1991), as the phosphorus concentration of plants follows the opposite pattern. This is indicated

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

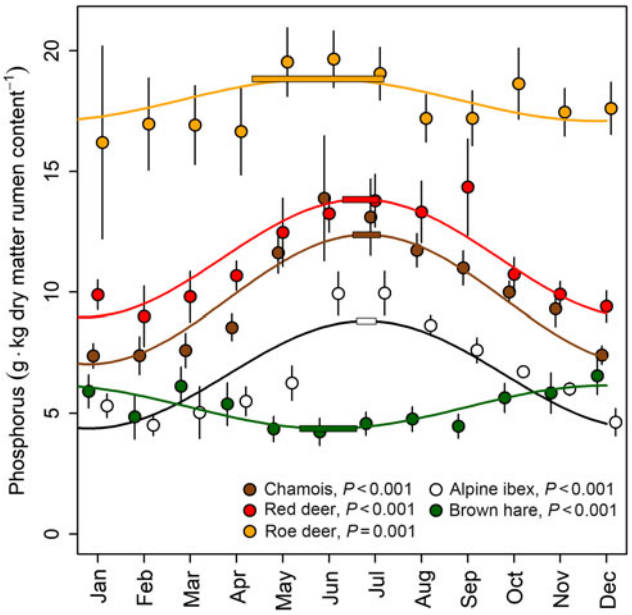

Figure 8 (colour online) Seasonal changes of phosphorus concentrations in the rumen content of four wild ruminant species and in the stomach content of the monogastric European brown hare (for methods, see Tataruch and Onderscheka, 1996). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as day of the year in radians. Lines represent periodic fits to the data; horizontal bars indicate 95% CI of peak or trough location, respectively.

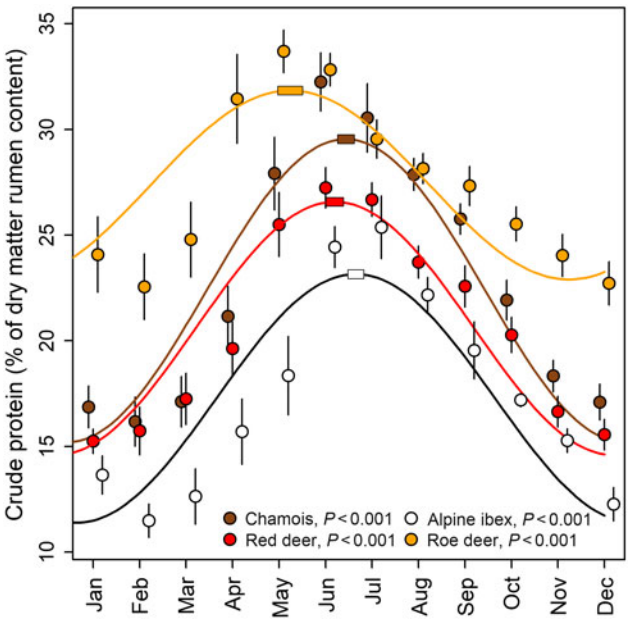

Figure 9 (colour online) Seasonal changes of CP in the rumen content of free-living wild ruminants (for methods, see Tataruch and Onderscheka, 1996). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modeling with sine (t) and cosine (t) as predictors with t as day of the year in radians. Lines represent periodic fits to the data; horizontal bars at peaks represent 95% CI of peak location.

by the phosphorus concentration in the stomach content of the monogastric European brown hare (Figure 8). From these data, it can be concluded that microbial growth is stimulated by increased phosphorus secretion into the rumen during

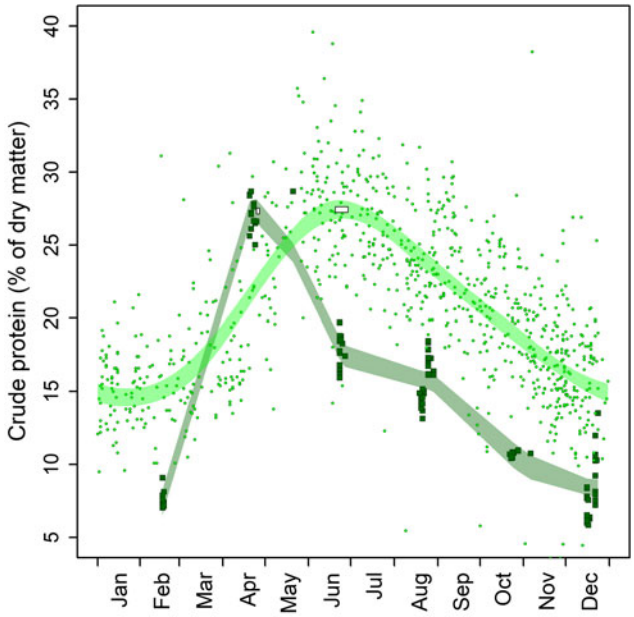

Figure 10 (colour online) Annual course of average CP concentrations in 10 most frequently eaten plants by red deer hinds that lived in a 45-ha enclosure close to natural conditions (squares, dark green; for details on methods, see Arnold *et al.*, 2015b), and in the stomach content of free-living red deer (circles, light green; same data as shown in Figure 9). Shaded areas indicate 95% CI of the overall mean courses determined by spline fitting (for details, see Wascher *et al.*, 2018). White horizontal bars within belts indicate 95% CI of peak location.

summer when the need for protein synthesis by rumen microbes is high, for example, for growth and reproduction (Peltier and Barboza, 2003; Knott *et al.*, 2005). In line with this interpretation, the highest phosphorus and CP concentrations are present throughout the year in the rumen content of roe deer (Figures 8 and 9), a concentrate-selecting species with limited ability for cell wall digestion.

With regard to endogenous phosphate recycling, increased phosphorus secretion by the host might be mediated by respective changes in salivary phosphate secretion and intestinal phosphate absorption. The expression of a sodium-dependent phosphate transporter has been demonstrated in the parotid gland of goats (Huber *et al.*, 2003) and in jejunal tissue (Huber *et al.*, 2002). It is therefore likely that a higher expression level of this transporter during summer increases the endogenous recycling of phosphorus in wild ruminants and hence produces the summer peak of phosphorus in the rumen content.

Altogether, peaks of CP in rumen contents, rather than seasonal changes of CP concentration in the feed, reflect a high microbial protein biosynthesis, governed by seasonal changes in host-derived gastrointestinal mechanisms (Figure 10). This view is supported by the aforementioned pattern of ruminal CP digestion, indicated by ammonia production. In red deer, the peak concentration of ammonia in rumen liquid occurs right after the peak of CP concentration in its most important feed plants, but clearly before the CP concentration in DM rumen content reaches its maximum (cf. peak CI of ammonia production, mid-April to mid-May, with Figure 10).

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

Conclusion

Profound phenotypical plasticity, evident in considerable seasonal changes of physiology and behavior, seems to be ubiquitous in wildlife species, including ruminants, living in seasonal environments of the northern hemisphere. Acclimatization to different living conditions during winter and summer is easily seen in the change from a winter to a summer coat, and vice versa. However, this visible seasonal acclimatization is only one feature of an all-embracing change taking place during the transition from a thrifty, catabolic winter phenotype into a highly productive, anabolic summer state, and encompasses the organismic and molecular levels (Arnold *et al.*, 2015a).

The major environmental cue governing this change is the photoperiod. It is well established that an endogenous circannual rhythm has a role in coordinating the expression of seasonal behaviors, such as reproduction, migration, hibernation, molt and the physiological and behavioral changes outlined above. A circannual biorhythm is maintained by cells residing in the hypothalamus and is entrained to time of the year by changes in pineal secretion of melatonin according to the photoperiod (Lincoln *et al.*, 2003). The importance of melatonin signal is revealed by the experimental administration of melatonin during summer, which caused in red deer a phase advance of the endogenous seasonal rhythm with advanced initiation of reproduction and seasonal reduction of voluntary feed intake (Heydon *et al.*, 1993).

We know meanwhile that seasonal differences in physiology are also present in domesticated animals, at least in primordial breeds (Brinkmann *et al.*, 2012; Brinkmann *et al.*, 2017; Riek *et al.*, 2017). The degree to which such differences exist in breeds of highly productive farm animals is far less understood and remains a scientific challenge for the future.

Acknowledgements

I am grateful to numerous hunters and, in particular, the Fonds für Umweltstudien Achenkirch for providing rumen content samples and information about body and organ mass of hunted animals. I thank Agnes Haymerle and Felix Knauer for conducting telemetry field work with chamois. The study of Taurus cattle was carried out by the Hortobágy National Park and supported by Zoo Cologne. For field work in Hortobágy, I thank Kristin Brabender, Viktor Molnar, Endre Sos, Gabrielle Stalder and Chris Walzer. My special thanks go to Thomas Ruf for his help with statistical analysis of periodic patterns; to Frieda Tataruch and the late Kurt Onderscheka for building up the reference value database of wildlife species, available at the Research Institute of Wildlife Ecology; to Renate Hengsberger for help with references and editing of the manuscript; and to Steve Smith for correcting the English. The author was supported by a grant from the Austrian Science Fund (FWF P 30061 B25).

W. Arnold 0000-0001-6785-5685

Declaration of interest

There are no potential conflicts of interest.

Ethics statement

All procedures outlined here were carried out in accordance with the respective national legislation. Corresponding ethics statements can be found in the cited publications. The studies of chamois and Taurus cattle were discussed and approved by the institutional ethics committee of the University of Veterinary Medicine Vienna.

Software and data repository resources

None of the data were deposited in an official repository

References

Arnold W, Beiglböck C, Burmester M, Guschlbauer M, Lengauer A, Schröder B, Wilkens M and Breves G 2015b. Contrary seasonal changes of rates of nutrient uptake, organ mass, and voluntary food intake in red deer (*Cervus elaphus*). American Journal of Physiology – Regulatory and Integrative Comparative Physiology 309, R277–R285.

Arnold W, Giroud S, Valencak TG and Ruf T 2015a. Ecophysiology of omega fatty acids: a lid for every jar. Physiology 30, 232–240.

Arnold W, Ruf T and Kuntz R 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) II. Energy expenditure. Journal of Experimental Biology 209, 4566–4573.

Arnold W, Ruf T, Loe LE, Irvine RJ, Ropstad E, Veiberg V and Albon SD 2018. Circadian rhythmicity persists through the Polar night and midnight sun in Svalbard reindeer. Scientific Reports 8, 14466.

Arnold W, Ruf T, Reimoser S, Tataruch F, Onderscheka K and Schober F 2004. Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). American Journal of Physiology – Regulatory and Integrative Comparative Physiology 286, R174–R181.

Aschenbach JR, Penner GB, Stumpff F and Gäbel G 2011. Ruminant Nutrition Symposium: role of fermentation acid absorption in the regulation of ruminal pH. Journal of Animal Science 89, 1092–1107.

Barboza PS, Peltier TC and Forster RJ 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiological and Biochemical Zoology 79, 497–513.

Beatty DT, Barnes A, Taylor E and Maloney SK 2008. Do changes in feed intake or ambient temperature cause changes in cattle rumen temperature relative to core temperature? Journal of Thermal Biology 33, 12–19.

Breves G and Schröder B 1991. Comparative aspects of gastrointestinal phosphorus metabolism. Nutrition Research Reviews 4, 125–140.

Brinkmann L, Gerken M and Riek A 2012. Adaptation strategies to seasonal changes in environmental conditions of a domesticated horse breed, the Shetland pony (*Equus ferus caballus*). The Journal of Experimental Biology 215, 1061–1068.

Brinkmann L, Riek A and Gerken M 2017. Long-term adaptation capacity of ponies: effect of season and feed restriction on blood and physiological parameters. Animal 12, 88–97.

Crater AR and Barboza PS 2007. The rumen in winter: cold shocks in naturally feeding muskoxen (*Ovibos moschatus*). Journal of Mammalogy 88, 625–631.

Crater AR, Barboza PS and Forster RJ 2007. Regulation of rumen fermentation during seasonal fluctuations in food intake of muskoxen. Comparative Biochemistry and Physiology A-Molecular and Integrative Physiology 146, 233–241.

DelGiudice GD, Mech LD, Kunkel KE, Gese EM and Seal US 1992. Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female deer in Minnesota. Canadian Journal of Zoology 70, 974–983.

Durand M and Kawashima R 1980. Influence of minerals in rumen microbial digestion. In Digestive physiology and metabolism in ruminants: proceedings of the 5th international symposium on ruminant physiology, held at Clermont-Ferrand, on 3rd–7th September, 1979 (ed. Y Ruckebusch and P Thivend), pp. 375–408. Springer Netherlands, Dordrecht.

Ferraris RP and Carey HV 2000. Intestinal transport during fasting and malnutrition. Annual Review of Nutrition 20, 195–219.

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press

Geiser F and Ruf T 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiological Zoology 68, 935–966.

Giacometti M, Bassano B, Peracino V and Ratti P 1997. Die Konstitution des Alpensteinbockes (*Capra i. ibex* L.) in Abhängigkeit von Geschlecht, Alter, Herkunft und Jahreszeit in Graubünden (Schweiz) und im Parco Nazionale Gran Paradiso (Italien). Zeitschrift für Jagdwissenschaft 43, 24–34.

Heydon MJ, Sibbald AM, Milne JA, Brinklow BR and Loudon ASI 1993. The interaction of food availability and endogenous physiological cycles on the grazing ecology of red deer hinds (*Cervus elaphus*). Functional Ecology 7, 216–222.

Hofmann RR 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78, 443–457.

Holand Ø 1994. Seasonal dynamics of digestion in relation to diet quality and intake in European roe deer (*Capreolus capreolus*). Oecologia 98, 274–279.

Huber K, Roesler U, Muscher A, Hansen K, Widiyono I, Pfeffer E and Breves G 2003. Ontogenesis of epithelial phosphate transport systems in goats. American Journal of Physiology – Regulatory and Integrative Comparative Physiology 284, R413–R421.

Huber K, Walter C, Schröder B and Breves G 2002. Phosphate transport in the duodenum and jejunum of goats and its adaptation by dietary phosphate and calcium. American Journal of Physiology – Regulatory and Integrative Comparative Physiology 283, R296–R302.

Hume ID 1989. Optimal digestive strategies in mammalian herbivores. Physiological Zoology 62, 1145–1163.

Hume ID, Beiglböck C, Ruf T, Frey-Roos F, Bruns U and Arnold W 2002. Seasonal changes in morphology and function of the gastrointestinal tract of free-living alpine marmots (*Marmota marmota*). Journal of Comparative Physiology B: Biochemical Systemic and Environmental Physiology 172, 197–207.

Irving L and Krog J 1955. Temperature of skin in the arctic as a regulator of heat. Journal of Applied Physiology 7, 355–364.

Knott KK, Barboza PS and Bowyer RT 2005. Growth in Arctic ungulates: postnatal development and organ maturation in *Rangifer tarandus* and *Ovibos moschatus*. Journal of Mammalogy 86, 121–130.

Kuntz R, Kubalek C, Ruf T, Tataruch F and Arnold W 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) I. Energy intake. The Journal of Experimental Biology 209, 4557–4565.

Lawler JP and White RG 2003. Temporal responses in energy expenditure and respiratory quotient following feeding in the muskox: influence of season on energy costs of eating and standing and an endogenous heat increment. Canadian Journal of Zoology 81, 1524–1538.

Lechner-Doll M, Kaske M and von Engelhardt W 1991. Factors affecting the mean retention time of particles in the forestomach of rumiants and camelids. In Physiological aspects of digestion and metabolism in ruminants (ed. T Tsuda, Y Sasaki and R Kawashima), pp. 455–482. Academic Press, London, UK.

Lincoln GA, Andersson H and Loudon A 2003. Clock genes in calendar cells as the basis of annual timekeeping in mammals – a unifying hypothesis. Journal of Endocrinology 179, 1–13.

Loudon ASI 1994. Photoperiod and the regulation of annual and circannual cycles of food intake. Proceedings of the Nutrition Society 53, 495–507.

Milner JM, Beest FM, Solberg EJ and Storaas T 2012. Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. Oecologia, 1–11.

Parker KL, Gillingham MP, Hanley TA and Robbins CT 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer in Alaska. Canadian Journal of Zoology 71, 1397–1404.

Pelletier F, Réale D, Grant D, Coltman DW and Festa-Bianchet M 2011. Selection on heritable seasonal phenotypic plasticity of body mass. Evolution 61, 1969–1979.

Peltier TC and Barboza PS 2003. Growth in an arctic grazer: effects of sex and dietary nitrogen on yearling muskoxen. Journal of Mammalogy 84, 915–925.

Peltier TC, Barboza PS and Blake JE 2003. Seasonal hyperphagia does not reduce digestive efficiency in an Arctic Grazer. Physiological and Biochemical Zoology 76, 471–483.

Reimoser S 2012. Influence of anthropogenic disturbance on activity, behaviour and heart rate of roe deer (*Capreolus capreaolus*) and red deer (*Cervus elaphus*), in context of their daily and yearly patterns. In Deer: habitat, behaviour and conservation (ed. AA Cahler), pp. 1–95. Nova Science Publishers, Hauppauge, NY, USA.

Riek A, Brinkmann L, Gauly M, Perica J, Ruf T, Arnold W, Hambly C, Speakman JR and Gerken M 2017. Seasonal changes in energy expenditure, body temperature and activity patterns in llamas (*Lama glama*). Scientific Reports 7, 7600.

Rutley BD and Hudson RJ 2000. Seasonal energetic parameters of free-grazing bison (*Bison bison*). Canadian Journal of Animal Science 80, 663–671.

Scholander PF, Hock R, Walters V, Johnson F and Irving L 1950. Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin 99, 237–258.

Short HL, Medin E and Anderson AE 1966. Seasonal variations in volatile fatty acids in the Rumen of Mule Deer. The Journal of Wildlife Management 30, 466–470.

Signer C, Ruf T and Arnold W 2011. Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. Functional Ecology 25, 537–547.

Stevens EC and Hume ID 1995. Comparative physiology of the vertebrate digestive system. Cambridge University Press, N.Y., Melbourne, Australia.

Stokstad E 2015. Bringing back the aurochs. Science 350, 1144–1147.

Tataruch F and Onderscheka K 1993. Gehalt an Ammoniak und flüchtigen Fettsäuren im Pansensaft von Rot-, Reh- und Gamswild. Wiener Tierärztliche Monatsschrift 80, 269–274.

Tataruch F and Onderscheka K 1996. Chemische Analysen der Panseninhalte von Steinwild in Graubünden. Zeitschrift für Jagdwissenschaft 42, 18–25.

Thompson DP, Barboza PS, Crouse JA, McDonough TJ, Badajos OH and Herberg AM 2019. Body temperature patterns vary with day, season, and body condition of moose (*Alces alces*). Journal of Mammalogy, 1–13.

Turbill C, Ruf T, Mang T and Arnold W 2011. Regulation of heart rate and rumen temperature in red deer: effects of season and food intake. Journal of Experimental Biology 214, 963–970.

Tyler NJC and Blix AS 1990. Survival strategies in arctic ungulates. Rangifer Special Issue 3, 211–230.

Wascher CAF, Kotrschal K and Arnold W 2018. Free-living greylag geese adjust their heart rates and body core temperatures to season and reproductive context. Scientific Reports 8, 2142.

Weiss CP, Gentry WW, Meredith CM, Meyer BE, Cole NA, Tedeschi LO, McCollum FT, III and Jennings JS 2017. Effects of roughage inclusion and particle size on digestion and ruminal fermentation characteristics of beef steers. Journal of Animal Science 95, 1707–1714.

https://doi.org/10.1017/S1751731119003240 Published online by Cambridge University Press