Review: Seasonal Differences in the Physiology of Wild Northern Ruminants

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Short title: Seasonal Wild Northern Ruminants

Abstract

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, i.e. 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, is during winter down-regulated 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 fibre, 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 the use of fat reserves, accumulated during summer, which become during winter a major metabolic fuel.

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 behaviour. 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 behavioural reactions in free-living animals continuously over long periods. These data unequivocally answered the long-standing question 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 hibernators and daily heterotherms (Arnold *et al.*, 2004, Arnold *et al.*, 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 1970-2006.

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 course of the year in physiological and behavioural parameters (Figure 1). Although these species do not hibernate or show daily torpor in the classical sense, they do become hypometabolic during the winter period, 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, Arnold *et al.*, 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^{-1}, annual range of f_H variation 30 beats • min^{-1} (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, is 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, Arnold *et al.*, 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 lib.* feeding prevent the decline towards 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 lib.* (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, Arnold *et al.*, 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 lib.* (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 considerable seasonal variation (Figure 5; similar changes are reported for Alpine ibex (Giacometti *et al.*, 1997), bighorn sheep (Pelletier *et al.*, 2011), 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 the 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 than other wild ruminants on a selective feeding strategy to enhance winter survival (Holand, 1994).

Secondly, 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). 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 in order to maintain a sufficient gradient of SCFA concentrations between rumen content and blood. Therefore, the rapid loss of mucosal mass 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 lib*. (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 the papillary epithelium (Hofmann, 1989). SCFA 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, especially the molar proportions of n-butyric, propionic, and n-valeric acid (Figure 7; Tataruch and Onderscheka, 1993). Similar changes are 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 fibre (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 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 the concentrations of fermentation products in the rumen liquid reflect the 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 the location of peak phosphorus concentration overlaps in each species with the CI of the location of peak concentration of crude protein in the rumen content (cf. Figure 8, Figure 9). Phosphorus is essential for growth and protein synthesis of the 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 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 summer when the need for protein synthesis by rumen microbes is high, e.g. for growth and reproduction (Peltier and Barboza, 2003, Knott *et al.*, 2005). In line with this interpretation, the highest phosphorus and crude protein concentrations are present throughout the year in the rumen content of roe deer (Figures 8,9), a concentrate selecting species with limited ability for cell-wall digestion.

With regard to the endogenous phosphate recycling, increased phosphorus secretion by the host might be mediated by respective changes in the salivary phosphate secretion and intestinal phosphate absorption. 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 crude protein in rumen contents, rather than seasonal changes of crude protein concentration in the feed, reflect 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 crude protein digestion, indicated by ammonia production. In red deer, peak concentration of ammonia in rumen liquid occurs right after the peak of crude protein concentration in its most important natural feed plants, but clearly before the crude protein concentration in dry matter rumen content reaches its maximum (cf. peak CI of ammonia production, mid-April to mid-May, with Figure 10).

Conclusion

Profound phenotypical plasticity, evident in considerable seasonal changes of physiology and behaviour, seems to be ubiquitous in wildlife species living in seasonal environments of the northern hemisphere, including ruminants. 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 level (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 behaviours, such as reproduction, migration, hibernation, molt, and the physiological and behavioural 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 the melatonin signal is revealed by the experimental administration of melatonin during summer, which causes in red deer, for instance, 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.

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Declaration of interest

There is no potential conflicts of interest.

Ethics statement

All procedures outlined here were carried out in accordance with the respective national legislation. Correspondent 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

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Figure captions

Figure 1 Seasonal change of heart rate, rumen temperature, and activity in six species of wild ungulates (roe deer (*Capreolus capreolus*): reanalysed data from (Reimoser, 2012); red deer (*Cervus elaphus*): reanalysed data from (Turbill *et al.*, 2011); chamois (*Rupicapra rupicapra*): unpublished data sampled 2009-2012 from nine male and seven female chamois (ages 4-12 years), living free in an alpine area in Upper Austria; Alpine ibex (*Capra ibex*): reanalysed data from (Signer *et al.*, 2011); Svalbard reindeer (*Rangifer tarandus platyrhynchus*): reanalysed data from (Arnold *et al.*, 2018); Taurus cattle: unpublished data from six >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% confidence intervals (CI) reflecting variation between individuals.

Figure 2 Seasonal change 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 modelling 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 the 95% CI of peak location.

Figure 3 Seasonal change of daily energy intake from pellets and natural vegetation of adult red deer hinds provided *ad libitum* with pellets (reanalysed 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 modelling: 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 Seasonal change 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 modelling 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 the 95% CI of peak location.

Figure 5 Seasonal change of body mass of free-living chamois, red deer, and roe deer. Body mass is plotted as a percentage of the 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, respectively. Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modelling 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 the 95% CI of peak location.

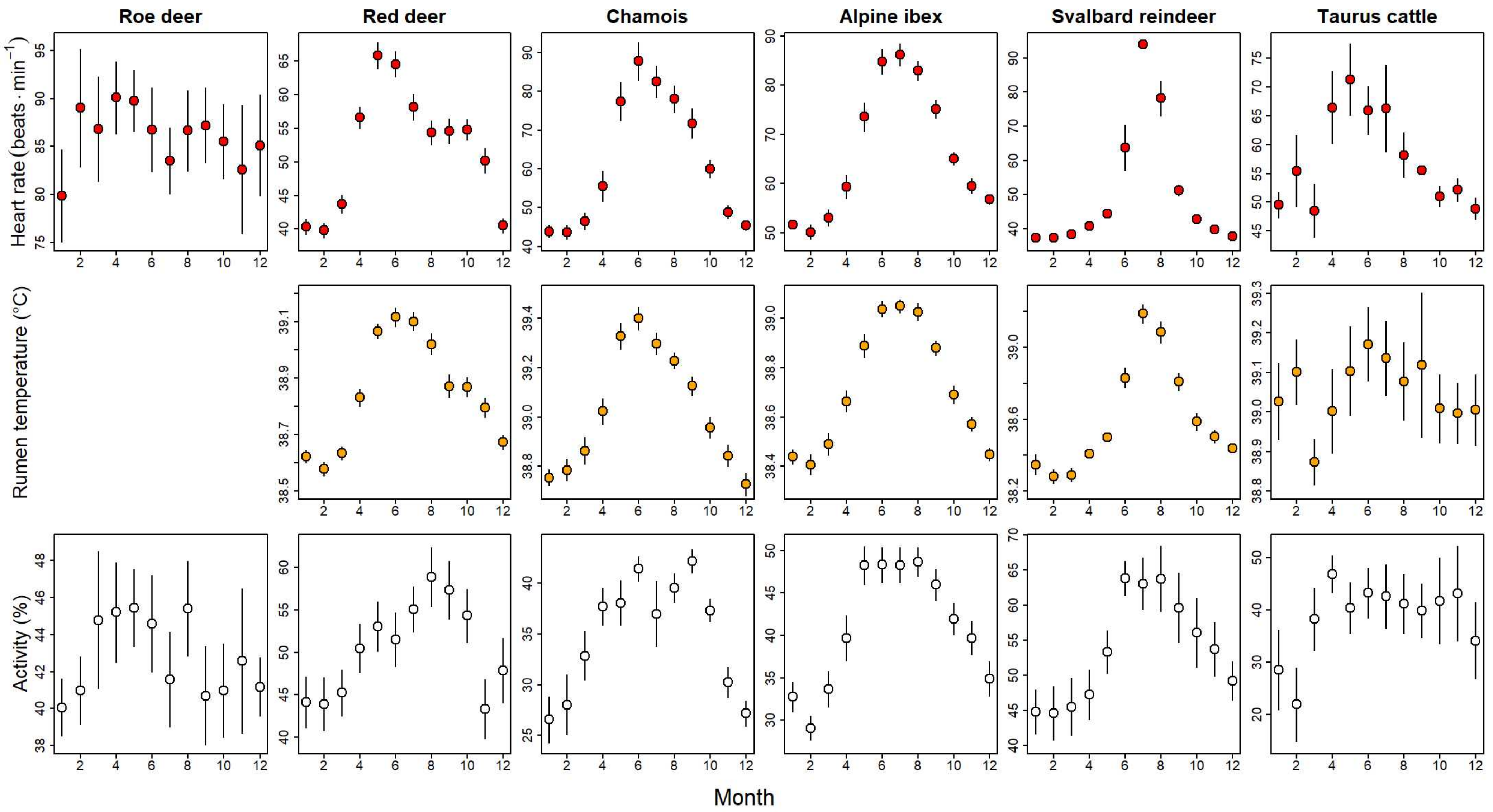
Figure 6 Seasonal change of total short chain fatty acid (SCFA) concentrations in the rumen liquid of free-living red and roe deer (for methods see Tataruch and Onderscheka, 1993). Plotted are monthly means with 95% CI, single values are indicated by a white dot. Significance of seasonal variation was tested by linear modelling 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 the 95% CI of peak location.

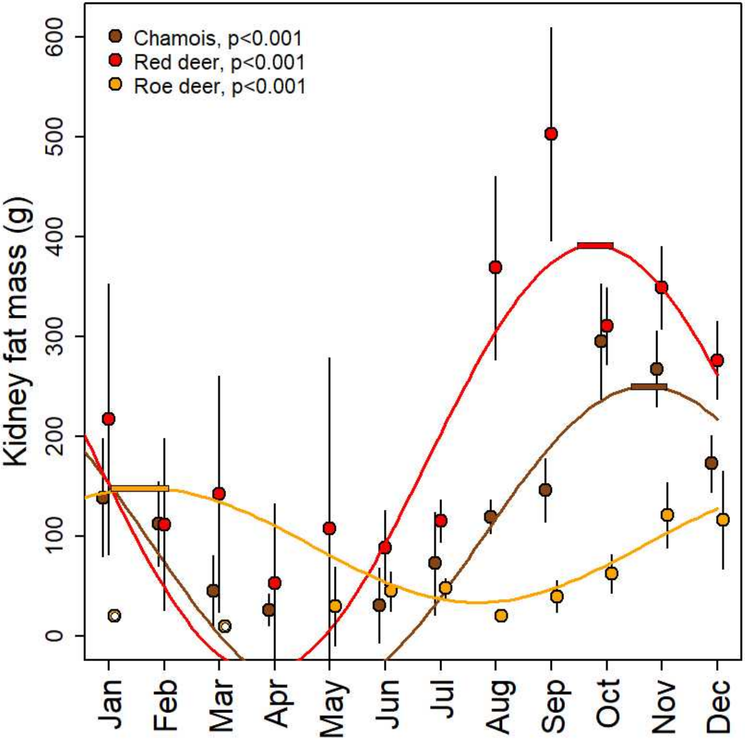
Figure 7 Seasonal change of the molar proportions of acetic (A), propionic (B), n-butyric (C), and n-valeric acid (D) in the total amount of short chain fatty acids in the rumen liquid of free-living red and roe deer (for methods see Tataruch and Onderscheka, 1993). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modelling 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 the 95% CI of peak location.

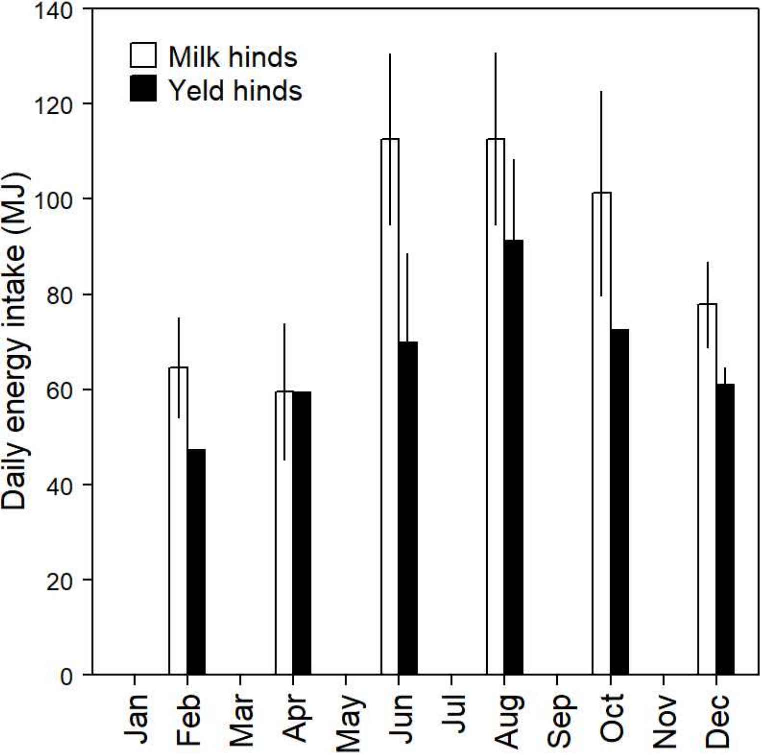
Figure 8 Seasonal change of phosphorus concentrations in the rumen content of four wild ruminant species and in the stomach content of the monogastric European brown hare (for methods see Tataruch and Onderscheka, 1996). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modelling 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 the 95% CI of peak or trough location, respectively.

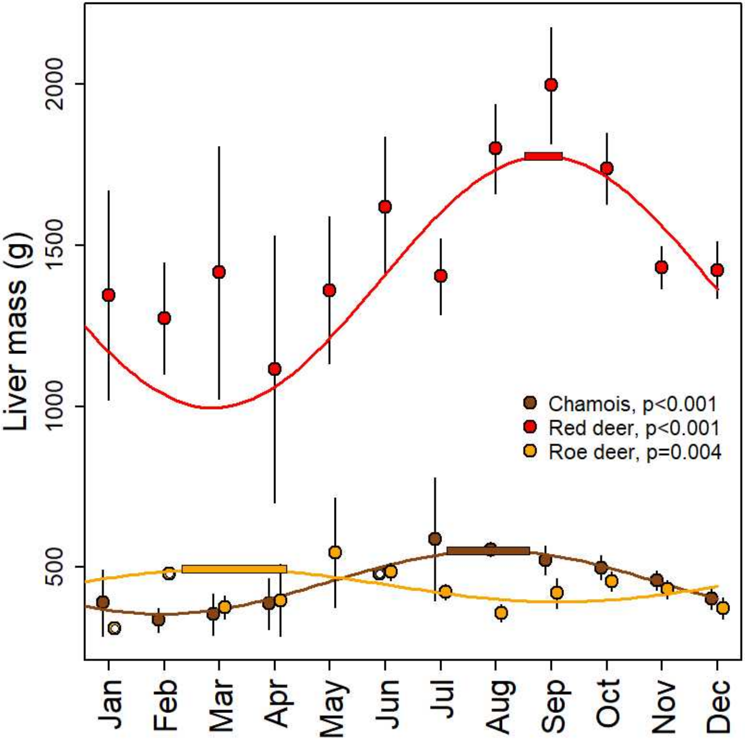
Figure 9 Seasonal change of crude protein in the rumen content of free-living wild ruminants (for methods see Tataruch and Onderscheka, 1996). Plotted are monthly means with 95% CI. Significance of seasonal variation was tested by linear modelling with sine (t) and cosine (t) as predictors with t as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

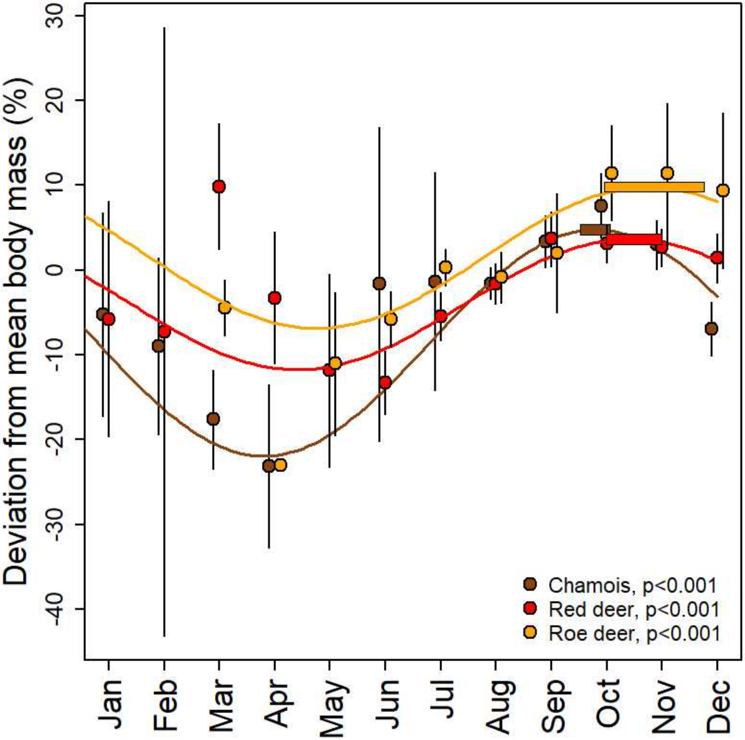
Figure 10 Annual course of average crude protein concentration in the 10 plants most frequently eaten by red deer hinds that lived in a 45 ha enclosure under close to natural conditions (squares, dark green, for details on methods, see Arnold *et al.*, 2015b), and in the stomach content of free-living 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.

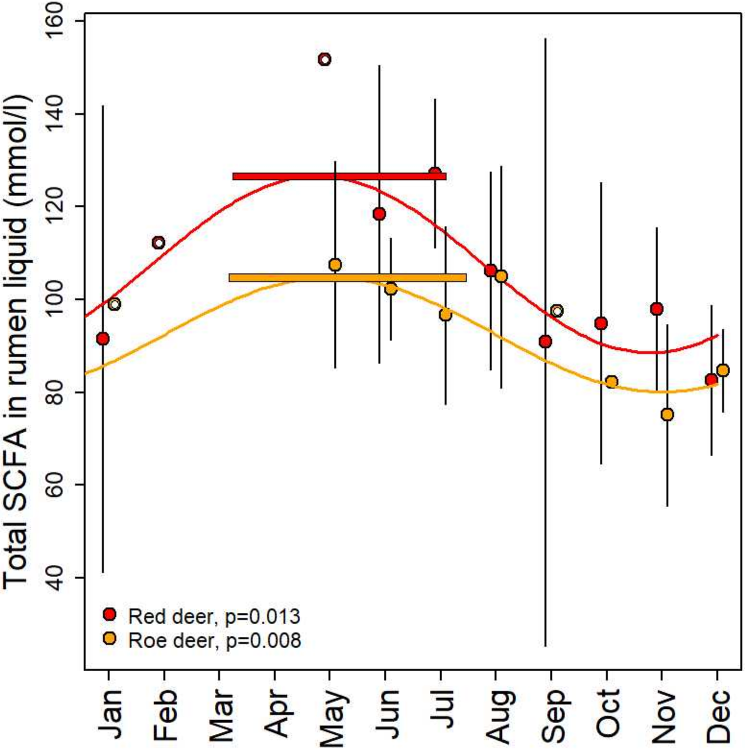

Roe deer
Red deer
Chamois
Alpine ibex
Svalbard reindeer
Taurus cattle
Heart rate (beats · min^{-1})
75 80 85 90 95
40 45 50 55 60 65
40 50 60 70 80 90
50 60 70 80 90
40 50 60 70 80 90
45 50 55 60 65 70 75
Rumen temperature (°C)
38.5 38.7 38.9 39.1
38.8 39.0 39.2 39.4
38.4 38.6 38.8 39.0
38.2 38.6 39.0
38.8 38.9 39.0 39.1 39.2 39.3
Activity (%)
38 40 42 44 46 48
40 45 50 55 60
25 30 35 40
30 35 40 45 50
40 45 50 55 60 65 70
20 30 40 50
2 4 6 8 10 12
Month

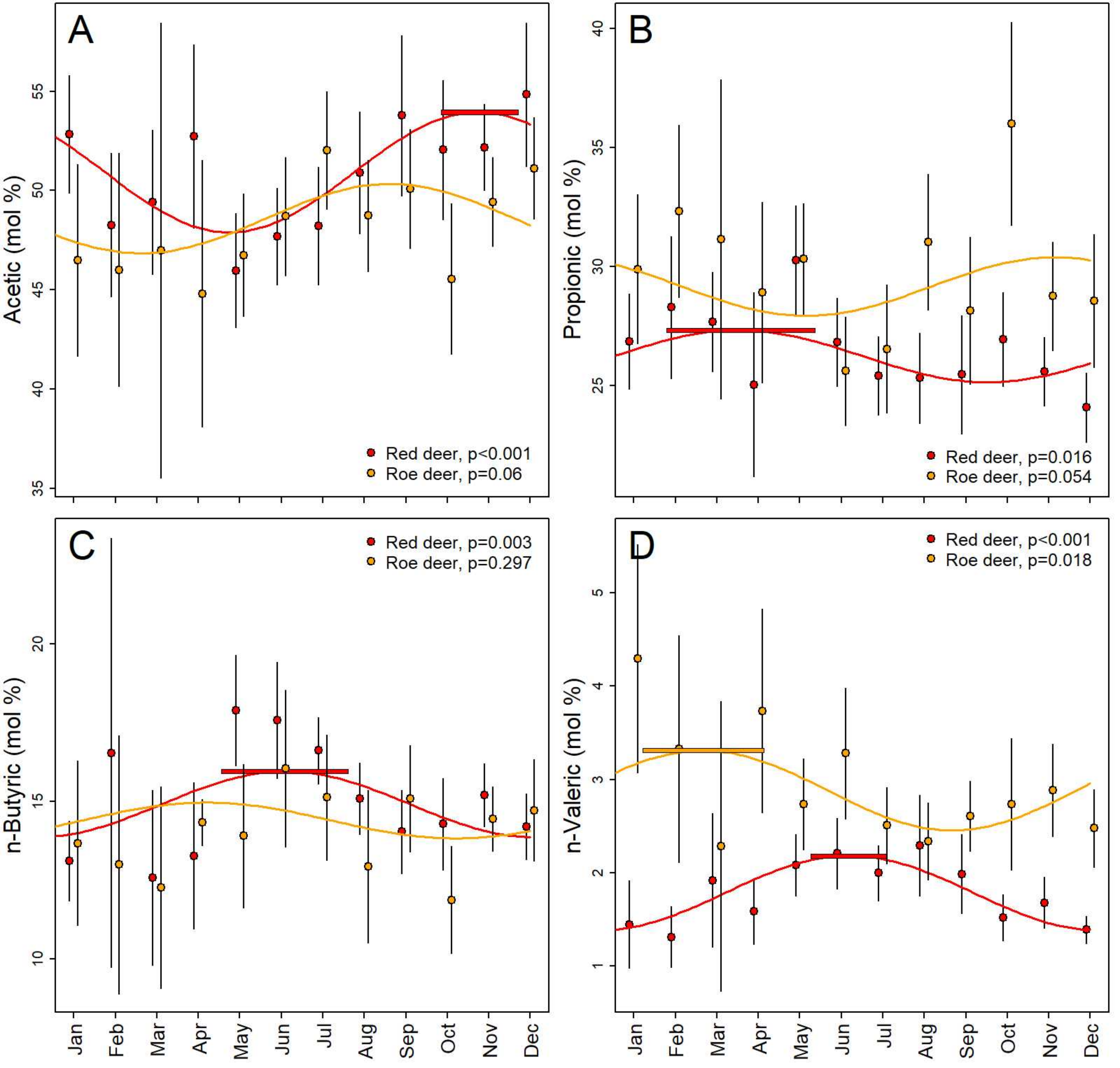

Chamois, p<0.001
Red deer, p<0.001
Roe deer, p<0.001
Kidney fat mass (g)
0
100
200
300
400
500
600
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

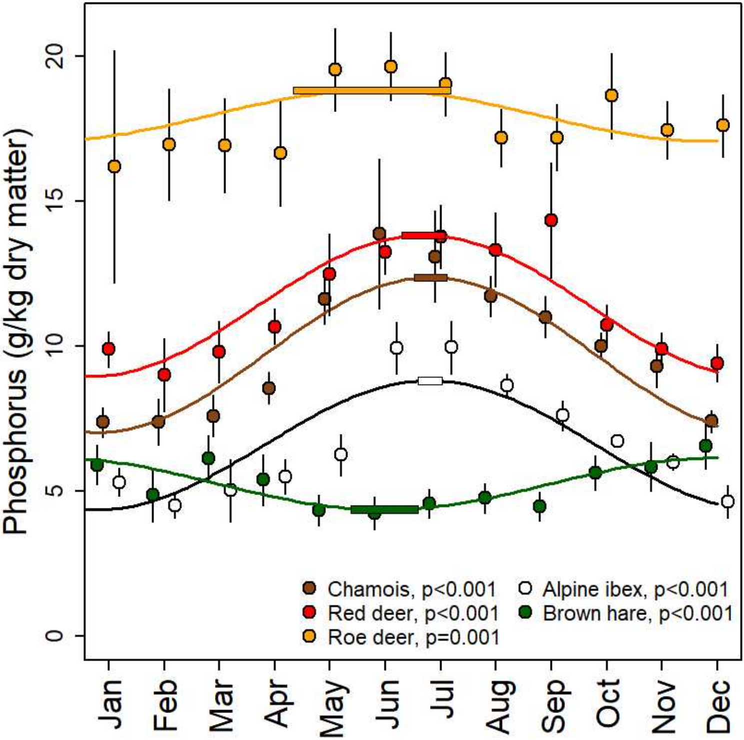

Milk hinds
Yeld hinds
Daily energy intake (MJ)
0
20
40
60
80
100
120
140
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

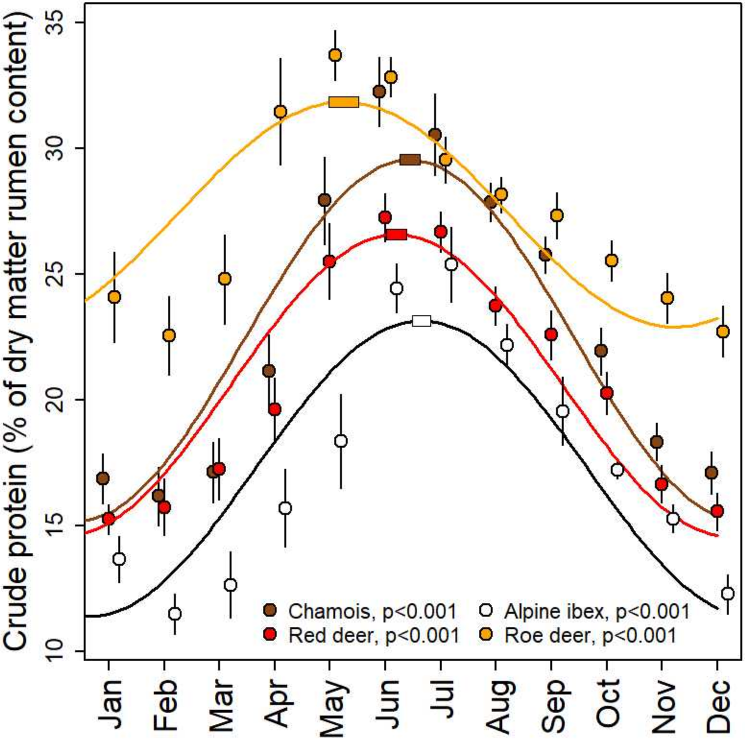

Liver mass (g)
2000
1500
1000
500
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Chamois, p<0.001
Red deer, p<0.001
Roe deer, p=0.004


Deviation from mean body mass (%)
30
20
10
0
-10
-20
-30
-40
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Chamois, p<0.001
Red deer, p<0.001
Roe deer, p<0.001

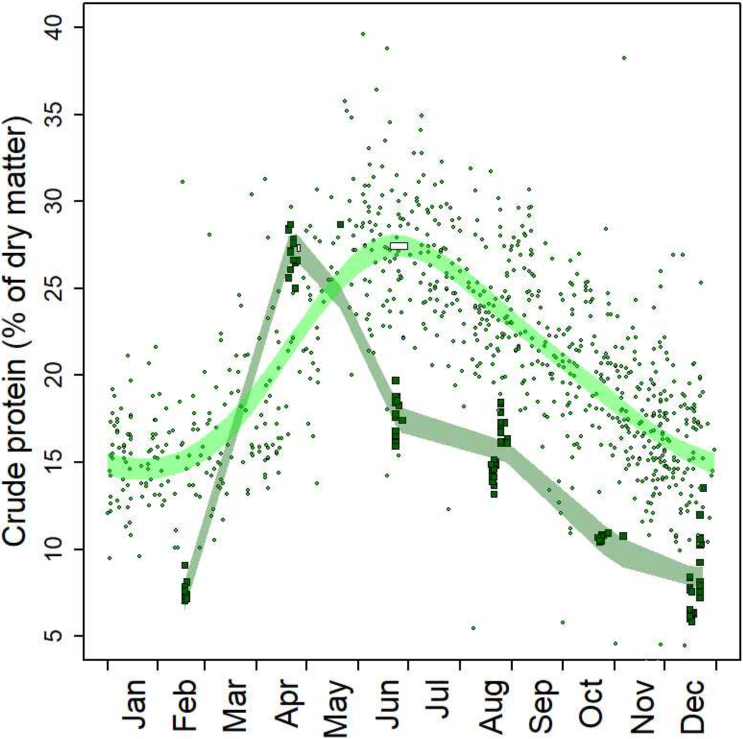

Total SCFA in rumen liquid (mmol/l)
160
140
120
100
80
60
40
Red deer, p=0.013
Roe deer, p=0.008
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

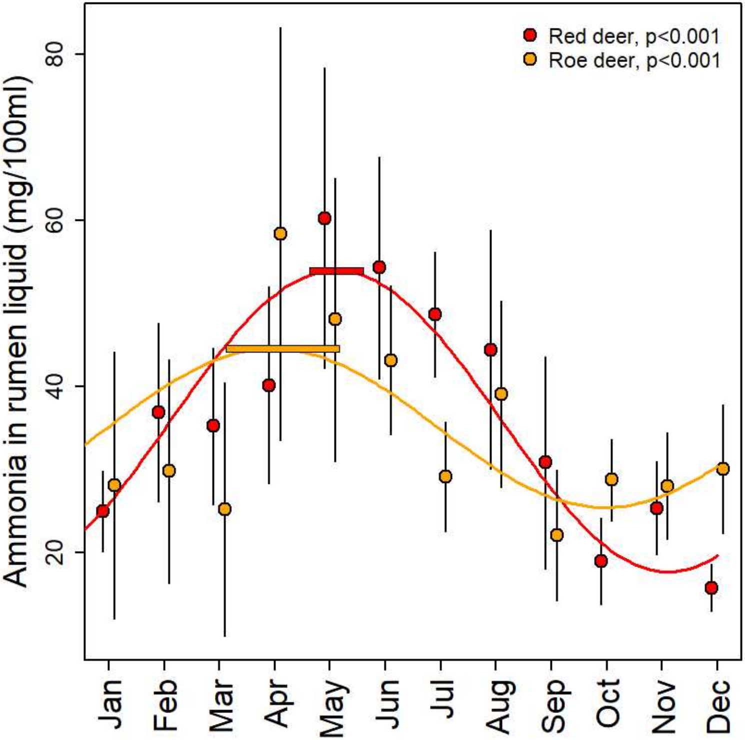

A
B
C
D
Acetic (mol %)
Propionic (mol %)
n-Butyric (mol %)
n-Valeric (mol %)
35
40
45
50
55
25
30
35
40
10
15
20
1
2
3
4
5
Red deer, p<0.001
Roe deer, p=0.06
Red deer, p=0.016
Roe deer, p=0.054
Red deer, p=0.003
Roe deer, p=0.297
Red deer, p<0.001
Roe deer, p=0.018
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Phosphorus (g/kg dry matter)
0
5
10
15
20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Chamois, p<0.001
Red deer, p<0.001
Roe deer, p=0.001
Alpine ibex, p<0.001
Brown hare, p<0.001



Crude protein (% of dry matter rumen content)
35
30
25
20
15
10
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Chamois, p<0.001
Red deer, p<0.001
Alpine ibex, p<0.001
Roe deer, p<0.001


Crude protein (% of dry matter)
5
10
15
20
25
30
35
40
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Red deer, p<0.001
Roe deer, p<0.001
Ammonia in rumen liquid (mg/100ml)
20
40
60
80
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec