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Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm

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Abstract Arctic Cervids face considerable challenges in sustaining life in a harsh and highly seasonal environment, and when to forage is a key component of the survival strategy. We predict that a cervid maximizes net intake of energy to change the duration of feeding-ruminating cycles depending on season, and pays no attention to light or other activity-entraining cues. Still, in periods of bad weather it may pay energetically to reduce exposure and heat loss. We investigated environmental impact on the seasonal and daily activity pattern of a food-limited, predator-free arctic deer, the Svalbard reindeer. We found that the reindeer indeed had season-dependent feeding-rumination intervals, with no distinct peaks in activity at sunrise and sunset, as would be expected if animals maximize energy intake rates in predator-free environments. However, they temporarily reduced activity when exposed to low temperature and increased precipitation during winter, possibly to conserve energy. We provide insight into the behavioural strategy of Svalbard reindeer which enables them to cope with such an extreme environment.

Introduction

Strategies of foraging animals typically involve a number of decisions regarding optimal diet composition, foraging

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Communicated by Jean-Michel-Gaillard.

We dedicate this paper to Nils Are Øritsland (born 1939) who died 24th of November 2006 of cancer. Norway lost a real “old-timer” with an extraordinary experience from the Arctic. We have lost a good colleague.

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space and how to distribute foraging between time periods (Schoener 1971; Owen-Smith and Novellie 1982; Owen-Smith 2002), issues that are typically interrelated. Optimal foraging theory (Charnov 1976; Stephens and Krebs 1986) focuses on how to maximize energy intake per unit of foraging time (under various constraints), but applies only for the time used for active foraging. Constraints to feeding time are critical, and even animals aiming at maximizing energy intake may use less than 50% of the time actually foraging. The main activity pattern of ruminants consists of a sequential series of foraging and rumination. The activity budget is mainly constrained by digestion time rather than searching time (Belovsky 1978; Owen-Smith and Novellie 1982), but short-term intake rate can also be an important limitation (Bergman et al. 2001). A major challenge facing terrestrial mammals in the high Arctic zone is the extreme seasonal periodicity in climate and food availability. Since plant quality is decisive for digestion time, digestion time typically increases during winter when plant quality is low (Cederlund 1989). Although arctic deer build up a substantial layer of fat during summer, they cannot survive a normal winter on fat alone. Most of the energy demand must be met by foraging (Tyler 1986b), and they need to continue with feeding and rumination.

Any departure from regular feeding–rumination cycles can be used to identify conditions when maximizing energy intake is not decisive. Deer are often reported to be crepuscular (i.e. activity peaking in the twilight periods at dusk and dawn; e.g., white-tailed deer: Beier and McCullough 1990; roe deer: Cederlund 1989), suggesting that factors other than maximizing energy intake play a role (Bergman et al. 2001). Similarly, climatic factors such as temperature have been shown to affect activity pattern in ruminants (Belovsky 1981; Belovsky and Slade 1986; Beier and McCullough 1990; Schmitz 1991; Demarchi and Bunnell 1995). They may experience temperature regimes where sheltering and lying down to reduce heat loss might be energetically beneficial, but is nevertheless not part of a feeding strategy focusing solely on maximization energy intake rates.

The Svalbard reindeer *Rangifer tarandus platyrhynchus* at 78° Northern latitude face an extreme climate, a continuous polar night in winter and continuous daylight in summer, both lasting for several months. An absence of a crepuscular activity pattern was recently reported in Svalbard reindeer, and this was related to the absence of a “zeitgeber” (any factor that plays a role in setting or resetting an internal biological clock) in this particular environment (van Oort et al. 2005). However, such an interpretation ignores the evolutionary aspect of behaviour. Crepuscular activity pattern is indeed expected mainly in areas with predators (Leuthold 1977). Insight from state-dependent modelling has shown that the type of activity pattern (such as nocturnal, diurnal or crepuscular) is predicted both to change over an evolutionary time scale and to be phenotypically plastic (Mangel and Clark 1986; Mcnamara and Houston 1986). For example, rabbits (*Oryctolagus cuniculus*) switched from a nocturnal to a diurnal activity regime when *mustelid* scent was added to foraging plots in an area where rabbits were subjected to night-time predation by pole cats (*Mustela putorius*; Bakker et al. 2005). The Svalbard reindeer is a particularly interesting case, as they have not been subjected to predation over their more than 5,000-year history on the archipelago (van der Knaap 1989). We can thus probably exclude predation as a determinant of the observed feeding pattern. In this study, we analyse the activity pattern of female Svalbard reindeer monitored over the entire annual cycle with ARGOS satellite collars, and use an evolutionary framework to understand their behaviour.

Based on energy intake maximization (H1), we predict that overall higher food availability, quality and basal metabolic rate during summer than during winter (Nilssen et al. 1984; Cuyler and Øritsland 1993) lead to (H1a) higher overall activity level during summer, (H1b) shorter duration of feeding-rumination bouts during summer, and (H1c) similar activity levels during light, twilight and dark (i.e., no peak in activity at sunrise and sunset as is common in most temperate deer) irrespective of season. Our prediction differs from the proximate explanation (predicting loss of stable diurnal activity cycles in the absence of a zeitgeber—Krüll 1976), as we predict an even activity pattern even in the presence of a zeitgeber [i.e., during twilight winter (29 January–5 April) and twilight autumn (8 September–14 November) periods]. If individuals instead maximize net energy assimilation (i.e., conserve energy during severe conditions) or avoid other stressors (H2), we predict that (H2a) activity will be negatively affected by low temperatures, strong wind and precipitation due to their effects on heat loss during winter only. If harassment by insects is important during summer (e.g., Hagemoen and Reimers 2002), we predict (H2b) increased activity at low temperatures and in windy and wet summer weather (since such weather reduces insect activity, and the reindeer presumably are within their thermo-neutral zone during summer).

Materials and methods

Study area

The study area is located in Colesdalen with side valleys, Nordenskiöld land, Svalbard (78° 0′ N, 16° 0′ E) and covers an area of ca. 100 km^2. The climate on Svalbard is polar (Major and Nagy 1972) and snow covers the study area from October or November to mid-June. Annual precipitation is low; ca. 300 mm per year (Hanssen-Bauer et al.

1990). Average temperature in the coldest month (February) is −16°C and average summer temperature in July is +6°C (http://www.met.no). In winter, temperature often increases to above freezing, and a layer of ice is produced as a combination of cold capacity in frozen soil and a following temperature decline. This limits reindeer access to the already poor winter range to an extent that may cause population crashes in some years (Kohler and Aanes 2004). The annual light cycle at this latitude is pronounced. From 6 April to 7 September there is no civil twilight, and the sun is continuously above the horizon from 19 April to 24 August. In autumn, the sun sets on 27 October and does not rise until 15 February, and between 15 November and 28 January there is not even civil twilight during mid-day.

There are no roads in the area. Human presence in summer is rare, but in winter a frequently used snowmobile track runs through a limited part of the study area. However, since the reindeer rapidly habituate to snow mobiles (Tyler 1991), any effect on activity pattern is probably minimal. The terrain within the study area is mountainous and moderately glaciated (Major and Nagy 1972) with peaks up to 1,000 m high, but with wide and even valley floors in between.

Svalbard is a marginal area for a deer species, and reproduction and survival is highly variable between years and linked to winter precipitation (Aanes et al. 2000; Albon et al. 2002) and icing events (Kohler and Aanes 2004; Chan et al. 2005). The overall population of Svalbard reindeer in the winter of 1982/1983 was estimated at 11,000 animals, including 400 animals in Colesdalen (Øritsland and Alendal 1986), and local counts (conducted by the Governor of Svalbard) indicate roughly the same population size today. The Svalbard reindeer is the only large herbivore on Svalbard. Natural predation on adult reindeer is virtually absent, as extremely few cases of polar bear killing reindeer are known (Derocher et al. 2000). The arctic fox (*Alopex lagopus*; Tyler 1986a) and the glaucous gull (*Larus hyperboreus*) may occasionally kill calves. No oestrid flies, known to be the worst stressors of reindeer and caribou (Morschel and Klein 1997; Morschel 1999) are present, but mosquitoes are locally abundant for short periods in summer. Harvesting by humans is restricted to an annual cull of 150–200 reindeer in the period 20 August–10 September (hunting statistics from the Governor of Svalbard).

The activity loggers and reindeer data

Six adult female Svalbard reindeer were equipped with ARGOS satellite collars (weight 1.4 kg; ca. 3 % of the winter body weight) in the time period 19 April 1998 to 30 December 1999. None of the animals were together when caught. Activity was measured with a mercury switch. The switch was active when the reindeer lowered its head (i.e., when grazing) and off when the head was upraised. The number of seconds the collar was active each hour (0 to 3,600) was temporarily stored in the collar. Before transmitting data to the satellite (to facilitate quick transfer), the hourly activity level was converted into one of seven groups depending on the number of seconds the collar was active; level 0: 0–450; level 1: 451–900; level 2: 901–1,350; level 3: 1,351–1,800; level 4: 1,801–2,250; level 5: 2,251–2,700; level 6: 2,701–3,150 and level 7: 3,151–3,600 s. Hourly activity level was monitored and stored for a 24-h period every 5th day during this period. The starting point of the 24-h interval was not fixed, and depended on when the ARGOS satellite was passing and available to receive data. Five of the six collars collected 100% of the data; ID 19183 missed 21 h during the period 7–8th February 1999, leading to a success rate of 99.3%. Automatic logging of activity corresponds closely to direct observations of activity (van Oort et al. 2004). The Svalbard reindeer live in loosely connected small groups (mothers with calves and possibly last year calves form the only stable bondage; R. Langvatn and S. Albon, unpublished data) that tend to be sexually segregated apart from during rut (Loe et al. 2006). The ARGOS collars also obtain spatial positions, simultaneously for all reindeer. Of all possible pairs of individual reindeer, 11 pairs were never closer than 200 m, while the remaining four pairs were separated by more than 200 m 99.2% of the time. This ensures that none of the individuals were members of the same group, and consequently excludes the possibility for social dependence in activity patterns.

Climatic data

Weather data from Svalbard airport (located ca. 20 km from the study area) was available from the Norwegian Meteorological institute (http://www.met.no). Temperature (average), precipitation (accumulated) and wind speed (average) were recorded every day for the full study period. We divided the year into five time periods based on a combination of light conditions and seasonality in temperature and snow conditions. Hours of sunset, civil twilight and sunrise for the exact location for the full year were obtained from U.S. Naval Observatory (http://www.aa.usno.navy. mil). The periods we chose were dark winter (15 November–28 January), twilight winter (29 January–5 April), light spring (6 April–15 June), light summer (16 June–7 September) and twilight autumn (8 September–14 November).

Statistical analyses

Periodicity in activity cycles

The activity data for each individual and season were split into separate time series. For the collar with 21 missing hours (ID 19183), we deleted the last 3 h from the same 24-h period to get a regular time series at the diurnal level. Each collar recorded activity hourly for one full day (24 h) every 5th day. We merged the batches of activity data into continuous time series for each individual within season (composing 30 series altogether for the six individuals and the five seasons). We removed linear trends in all the time series before using the function spec.pgram in R (R Development Core Team 2006) to calculate the periodogram for each individual and season combination. Thereafter, we plotted periodograms, revealing peaks that reflect cyclic trends in the activity patterns. If individual activity is cyclic across more than one time span, multiple peaks will be present. The dominating frequency of individual activity cycles is displayed in the periodograms (See Fig. S1). The period of each cycle (i.e., the time between each activity bout) is a more meaningful value for us. From physics we know that the frequency and the period of a cycle are reciprocal values. We consequently found the period (in hours) by dividing 1 by the peak frequency (Fig. S1).

Activity peak around sunrise and -set

To test for peaks in activity around sunrise and sunset (cfr. H2), we first restricted the analysis to the two seasons where the sun does actually rise and set—termed “twilight winter” and “twilight autumn” periods (see above for dates). Secondly, we restricted activity data to 9-h periods around sunrise and sunset, to investigate activity peaks around rise and set respectively (cfr. H2). We created a variable called “time offset” by subtracting observation time from time of sunrise and sunset (rounded to closest hour). Thereafter, we used GAM models (Woods 2006) to explore the relationship between level of activity (binary response variable; 1 or 0; see below) and the predictor variable “time offset” (a continuous variable from −5 to 5). The variable “time offset” was fitted with a spline function to allow for a flexible relationship between the two variables. We used these GAM plots to visually assess the presence of activity peaks at time 0 (sunrise and sunset).

Environmental effect on activity

The activity loggers assigned the level of activity into seven groups. The distribution of the activity data approximated to neither a normal nor a Poisson distribution (Fig. S2 in the electronic appendix). When analysing environmental effects on activity, we therefore chose to transform the seven-level activity data into only two groups to get a binomial distribution (by assigning the category “active” to all activity levels > 0 and only keeping the level 0 as “non-active”). This is also biologically meaningful, since ca. 70% of the observations are now coded active (1) and 30% non-active (0), fitting well with earlier observations of the activity pattern of Svalbard reindeer (Kastnes 1979). Thereafter, we fitted a generalized linear model (GLM) with a logit link, with hourly activity as the response variable and various environmental variables as predictor variables. Predictor variables were: (1) time period (dark winter, twilight winter, light spring, light summer and twilight autumn; see above for dates), (2) hour (0–23) up to fifth order, (3) identity of the animal, (4) wind speed (m/s; daily average), (5) temperature (°C; daily average), (6) precipitation (mm; accumulated per day,) and (7) two-way interactions (Table 1). The effect of hour is fitted up to fifth order to account for multiple activity peaks within a day. We also modelled the effect of hour with a spline-function (even more flexible than a fifth order term in a linear modelling framework) in a GAM model, retaining all other variables as presented here. None of the other parameter estimates in the model changed notably. All continuous predictor variables were standardized to facilitate direct comparisons of effect size. The best model was found from selection based on the AIC criterion (Burnham and Anderson 1998) among a set of a priori candidate models (Table S1 in the electronic appendix).

Finally, we assessed the model fit (goodness-of-fit tests, GOF; Agresti 2002) by (1) transforming continuous variables into a 10-class categorical variable, before (2) comparing the Pearson residuals with a Chi-square with the residual number of degrees of freedom. We assume that a good fit of simple models (including only one predictor variable) indicate that extended models also fit well. All GOF P values were >0.4, suggesting that the models captured the data adequately and did not show any sign of overdispersion, i.e., that residual deviance approximated the residual degrees of freedom (Agresti 2002).

In GLM, we always report differences between levels with “treatment” contrasts, i.e., comparing levels of a factor with a reference level. All analyses were performed using the software R (R Development Core Team 2006).

Results

As predicted (H1a), the activity level was much higher in summer (June to September) than the rest of the year (Fig. 1; Table 1). All of the six female reindeer showed strong activity cycles that varied among seasons, with low variability among individuals (Fig. S1 in the electronic appendix). During summer, activity cycled with a periodicity of 5 h, while the period was ca. 7 h during the rest of the year (Fig. 2), consistent with prediction H1b. All individuals had one cycle that dominated. In no case was a 24-h activity cycle detected (Fig. S1 in the electronic appendix). Prediction H1c was partly supported, since the reindeer did

Table 1 The most parsimonious model for the relationship between environmental variables and the probability to be registered active in six female Svalbard reindeer

	Parameter estimate	95% CI
Intercept	1.017	0.866; 1.17
Season (light spring–dark winter)	0.165	0.00590; 0.324
Season (light summer-dark winter)	1.65	1.22; 2.08
Season (twi autumn-dark winter)	0.557	0.399; 0.714
Season (twi winter–dark winter)	−0.317	−0.531; −0.104
Hour	0.247	-0.969; 1.46
Hour^2	−7.11	−14.4; 0.239
Hour^3	25.1	6.98; 43.3
Hour^4	−30.9	−50.3; −11.5
Hour^5	12.6	5.22; 20.1
ID (19182–19181)	0.0611	−0.0659; 0.188
ID (19183–19181)	−0.105	−0.230; 0.0197
ID (19184–19181)	0.275	0.145; 0.406
ID (19185–19181)	0.542	0.406; 0.678
ID (19186–19181)	0.532	0.396; 0.667
Temperature	0.416	0.318; 0.514
Precipitation	−0.113	−0.187; −0.0395
Temperature × season (light spring–dark winter)	0.207	0.0657; 0.348
Temperature × season (light summer–dark winter)	−0.767	−1.12; −0.417
Temperature × season (twi autumn–dark winter)	0.0459	−0.134; 0.225
Temperature × season (twi winter–dark winter)	−0.392	−0.576; −0.209
Precipitation × season (light spring–dark winter)	0.239	0.0152; 0.462
Precipitation × season (light summer–dark winter)	0.293	0.107; 0.478
Precipitation × season (twi autumn-dark winter)	0.0846	−0.0115; 0.181
Precipitation × season (twi winter–Dark winter)	0.198	−0.269; 0.665
Hour × season (light spring–dark winter)	0.137	−0.820; 1.09
Hour × season (light summer–dark winter)	0.204	−0.905; 1.31
Hour × season (twi autumn–dark winter)	0.299	−0.712; 1.31
Hour × season (twi winter–dark winter)	0.454	−0.668; 1.58
Hour^2 × season (light spring–dark winter)	2.21	−0.161; 4.57
Hour^2 × season (light summer–dark winter)	1.39	−1.37; 4.16
Hour^2 × season (twi autumn–dark winter)	1.43	−1.06; 3.92
Hour^2 × season (twi winter–dark winter)	1.84	−0.932; 4.61
Hour^3 × season (light spring–dark winter)	−2.11	−3.62; −0.591
Hour^3 × season (light summer–dark winter)	−1.53	−3.30; 0.242
Hour^3 × season (twi autumn–dark winter)	−1.74	−3.33; −0.156
Hour^3 × season (twi winter–dark winter)	−2.21	−3.98; −0.436

All continuous variables are standardised to allow for direct comparison. The effects of categorical variables are relative to the reference level given in the table (e.g., dark winter for the effect of season); see Table S1 for AIC values of the presented and all other candidate models

not show a crepuscular activity pattern. However, they were more active in the light than the dark part of the 24-h day (not predicted by H1c). Restricting the analyses to periods with daily changes in light conditions, we found an effect of light on level of Svalbard reindeer activity both in the period "twilight winter" (including light: AIC = 2,213.9; excluding light: AIC = 2,274.2, ΔAIC = 60.3), and in the period "twilight autumn" (including light: AIC = 3,353.8; excluding light: AIC = 3,451.2, ΔAIC = 97.4). In the "twilight winter" period the reindeer were more active during the light part [79% of the time; estimate = 0.891; 95% CI = (0.653, 1.13)] and twilight [75% of the time; estimate = 0.683; 95% CI = (0.403, 0.964)] than the dark part of the 24-hr day (61%). There was no difference between light and twilight hours [estimate = 0.207; 95% CI = (−0.107, 0.521)]. In autumn, the reindeer were more active in daylight (92% of the time) than in both twilight hours [88%; estimate = 1.06; 95% CI = (0.832, 1.30)] and dark hours [79%; estimate = 0.434; 95% CI = (0.120, 0.749)]. We found no distinct peaks in activity at sunrise

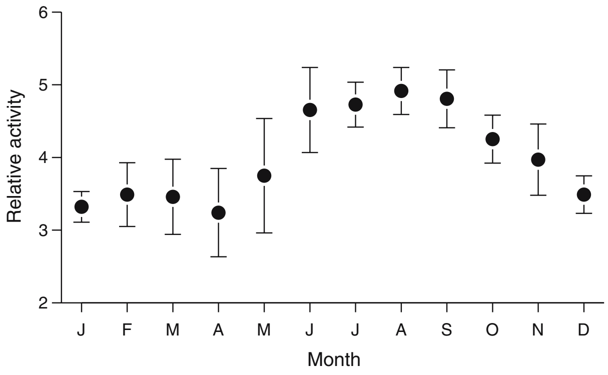

Fig. 1 Mean monthly activity level (relative scale) of six female Svalbard reindeer. *Error bars* represent 95% confidence limits

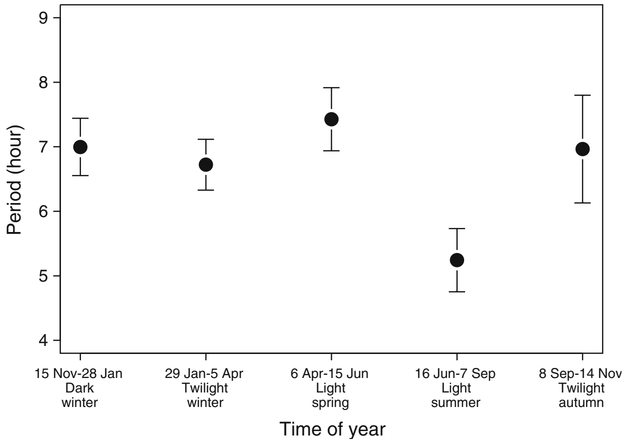

Fig. 2 Average periodicity (with 95% CI, adjusted for small sample size, $n = 6$) in activity cycles of six female Svalbard reindeer at five seasons. The five seasons (each *panel*) were chosen by a combination of light conditions and seasons resulting in: dark winter (15 November–28 January), twilight winter (29 January–5 April), light spring (6 April–15 June), light summer (16 June–7 September), twilight autumn (8 September–14 November). See Materials and methods for estimation of periodicity in activity cycles

and sunset in the "twilight winter" and "twilight autumn" periods (Fig. S4 in the electronic appendix). See Fig. S3 in the electronic appendix for seasonal and individual variation in daily activity pattern.

As predicted (H2a), temperature had a positive and precipitation a negative effect on level of activity during winter (Table 1). Hypothesis H2b was also supported, as temperature and precipitation influenced activity also during summer, but in opposite directions than during winter (a negative effect of temperature and positive effect of precipitation; Table 1). Contrary to the predictions from H2a and H2b, we found no effect of wind speed on the level of activity in any season (no main effect of wind speed or interaction with season included in the best model; Table S1 in the electronic appendix).

Discussion

We have tested hypotheses regarding the activity pattern of a deer living in the high Arctic; the Svalbard reindeer. Due to low variability among individuals, the sample size of six female Svalbard reindeer was sufficient to demonstrate conclusive patterns in seasonal and daily activity rhythms.

The overall level of activity was higher in summer than in winter (see also Kastnes 1979), as reported for a number of Cervid species (Cederlund 1981, 1989; Georgii 1981) as well as in the resident Svalbard ptarmigan *Lagopus mutus hyperboreus* (Reierth and Stokkan 1998). In accordance with earlier studies of *Rangifer* species (Erriksson et al. 1981; Skogland 1984; Maier and White 1998; Colman et al. 2001), we found a polycyclic activity pattern in Svalbard reindeer (5-h periods in summer and 7-h periods the rest of the year). Caribou also expressed a higher number of activity cycles per day during summer (7.5 and 4.5 in captive and wild caribou) than during winter (5.5 and 4 in the same groups) (Maier and White 1998), similar to other cervids (Cederlund 1989). Increased digestion time during winter (Erriksson et al. 1981) because of lower plant quality (Hanley 1982; Owen-Smith and Novellie 1982; Demment and Van Soest 1985; Cederlund 1989) is probably a prominent cause for lower overall activity and longer activity cycles during winter than summer.

We demonstrate that the Svalbard reindeer are not crepuscular, but rather fit with a diel activity pattern (sensu Blight et al. 1976). They do have a slight bias (ca. 15%) towards being diurnal, but are highly active also during night time (more than 60% of the time). A diel activity category is expected for both fore- and hindgut fermentors (Staaland et al. 1979) that maximize their foraging efficiency (Leuthold 1977; Kay and Staines 1981; Staaland et al. 1988; Maier and White 1998). Reindeer in general appear to be more night-active than most other ruminant species (Colman et al. 2001) and do not increase activity level at sunrise or sunset (Maier and White 1998; Colman et al. 2001; but see Erriksson et al. 1981, who report a tight relationship between sunrise and onset of activity in reindeer, and that diurnal activity predominates). This contrasts with the pattern of many northern deer species, who show distinct activity peaks at sunrise and sunset at least in some parts of the year (Cederlund 1981; Georgii 1981, 1984, Bowyer 1981; Georgii and Schröder 1983; Hamr and Czakert 1986; Cederlund 1989; Beier and McCullough 1990; Green and Bear 1990; Hansen 1996). For African ungulates, the ratio of daytime to nighttime feeding declined with increasing body mass (Owen-Smith 1988). Since most large African predators are nocturnal, and since smaller prey are more vulnerable (Sinclair et al. 2003), the megaherbivores are fairly safe during night, while they can then also avoid heat stress during the day (Owen-Smith 1988).

Clearly, fairly detailed insight into predator activity, avoidance behaviour in relation to habitat, and other environmental stressors are needed to gain better insight into how the contrasting activity patterns have evolved, and how flexible they are in other areas than Africa.

During winter, Svalbard reindeer altered their activity pattern with respect to temperature and precipitation in directions appropriate to energy conservation, which can be seen as part of a survival strategy (Cuyler and Øritsland 1993). The positive effect of temperature, and the negative effect of precipitation on activity level during winter, are to be expected if the reindeer seek shelter and stay inactive to reduce heat loss (due to increased wind chill, when standing upright and active than when lying down; Moen 1973; Cuyler and Øritsland 1986; Conradt et al. 2000). The effect of precipitation (mainly snow fall) may also be linked to instantly reduced availability of forage. The lack of an effect of wind on activity during winter is contrary to what might be expected from the wind-chill hypothesis, but agrees with the wind-resistant and high insulating properties of the Svalbard reindeer fur (Øritsland 1974; Cuyler and Øritsland 2002a, b, 2004). Summer temperature is often linked to ecto-parasite burden, and many populations of *Rangifer* are harassed by insects (e.g., Hagemoen and Reimers 2002), which may impact on body weight development (Weladji et al. 2003). The oestrid flies which are known to severely affect the activity patterns of reindeer and caribou elsewhere (Morschel and Klein 1997; Morschel 1999; Hagemoen and Reimers 2002) are absent in Svalbard. Since mosquitoes may be locally abundant for a short period in mid to late summer in our study area, we cannot exclude the possibility that the summer climate effect is mediated through harassment by mosquitoes. We regard heat stress in Svalbard in the observed temperature range (the highest recorded temperature during the study was 18.4°C) to be unlikely.

Our study provides insight into the behavioural strategy of Svalbard reindeer which enables them to cope with such an extreme environment. Reindeer showed season-specific, feeding–rumination periods, and no distinct peaks in activity at sunrise and sunset even when a “zeitgeber” was present, as might be expected if aiming to maximize energy intake throughout the year in a predator-free environment. However, they do temporarily reduce feeding time when exposed to extremely low temperatures and precipitation in winter. This conforms with the suggestions of Cuyler and Øritsland (1986, 1993) and is expected for an arctic deer whose time budget is not constrained by predation but mainly by optimising net energy assimilation through foraging activities.

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