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Influence of Climate and Daylength on the Activity Budgets of Feral Goats (*Capra hircus*) on the Isle of Rum, Scotland

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Abstract: Daytime activity budgets of feral goats (*Capra hircus*) were studied in 1981, 1982 and 2000 on the Isle of Rum, northwest Scotland. This paper analyzes the influence of key weather variables (temperature and rainfall) and seasonal variations in daylength on daytime activity budgets. This study showed that the percentage of daytime spent in feeding by feral goats on Rum Island decreased with average monthly temperature, while the percentage of daytime spent in lying increased and rainfall had no significant effects on the percentage daytime spent in feeding or lying. The daylength varied greatly from January to December with the longest daylength being in June and July, and the shortest one in December and January. The amount of daytime spent feeding decreased from summer to winter, although the percentage of daytime spent feeding increased greatly from summer to winter. The seasonal variations in daylength seem to be an important factor in constraining feral goats' activity, especially in the cold and wet winters when forage biomass and quality are both at their lowest level. We discuss the influence of such constraining effects on the forage intake of these goats and their winter survival rate, as well as its implication for population regulation of these goats.

Key words: Weather; Activity budget; Daylength; Feral goat; Rum Island

气候与白昼长度变化对苏格兰拉姆岛上野化山羊种群日活动节律的影响

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摘要: 对生活于苏格兰西北部拉姆岛上的野化山羊(*Capra hircus*)种群在 1981、1982 和 2000 年三年中的日活动节律进行了分析研究。详细分析了两个主要气象因素(温度和降水)以及昼长季节变化对该种群动物的日活动节律的影响。研究结果表明, 拉姆岛上野化山羊的日取食活动时间百分比随月平均温度上升而显著下降, 但卧息活动时间百分比随月平均温度的上升而显著上升, 而降水则对二者无显著影响。拉姆岛所在地区的昼长季节性变化明显, 每年 6、7 月白昼时间最长, 而 12、1 月最短。由于受昼长季节变化影响, 尽管该山羊种群的日取食活动时间百分比随季节变化而由夏季到冬季增加, 但其真正用于取食活动的白昼时间由夏季到冬季反而减少。研究表明, 白昼时间长短的季节变化是制约该山羊种群取食活动的一个重要因素, 尤其是在食物匮乏而天气寒冷、阴湿的冬季。进而探讨了这种制约作用对其冬季取食量和冬季存活率的影响, 以及对种群数量的调节意义。

关键词: 天气; 活动节律; 白昼长度; 野化山羊; 拉姆岛
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Animals living under stressful climatic conditions are likely to face severe constraints on their activities

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that may have adverse consequences for their ability to balance energy and nutrient budgets. Numerous studies have demonstrated that environmental variables such as weather can influence animal's behaviour and activity patterns, and such influence can be either direct (through day-to-day changes in weather) or indirect (through the seasonal effects of climate on habitat conditions) (Leuthold, 1977; Brindley et al, 1989; Roberts & Dunbar, 1991; Dunn et al, 1988; Mörschel & Klein, 1997; McKnight, 1998; Owen-Smith, 1998; Olson & Wallander, 2002). For example, some studies have found animals in their natural environments alter their activity schedules in response to thermoregulatory needs (baboon *Papio papio*, Altmann & Altmann, 1970; Hill, 1999; gelada *Theropithecus gelada*, Iwamoto & Dunbar, 1983; Cape buffalo *Syncerus caffer caffer*, Winterbach & Bothma, 1998; red kangaroo *Magaleria rufa*, Russell, 1971; red deer *Cervus elephus*, Staines, 1976). Rainfall has been identified as the single most important factor in determining range use by Arabian oryx (*Oryx leucoryx*) and is of great importance for their reproductive success in their desert habitats (Stanley & Price, 1989; Corp et al, 1998). Hepp (1985) reported that gadwalls (*Anas strepera*) and green-winged teals (*Anas crecca carolinensis*) increased foraging intensity as daylength decreased through the fall and winter, both as a response to reduced time available for feeding and to avoid feeding after dark when temperature is low and thermoregulatory cost is high.

In addition, climatic factors (especially temperature and rainfall) have been reported to have both direct and indirect effects on survival of both adult and young individuals, and on population dynamics of some ungulates (Boyd, 1981; Albon & Clutton-Brock, 1988; Portier et al, 1998; Saether et al, 2002; Wang et al, 2002; Weladji & Holand, 2003; Kumpula & Colpaert, 2003; Ogutu & Owen-Smith, 2003; Jacobson et al, 2004). Variations in summer temperature can directly influence caribou (*Rangifer arcticus*) behaviour and activity patterns in Alaska and have been considered a factor that may have contributed to (or triggered) the species' population decline in recent years (Mörschel & Klein, 1997).

An understanding of how climatic factors affect an animal's activity budgets may help us understand the mechanisms underlying relationships between weather and population dynamics. Although a number of studies have explored the influence of weather on activity patterns in both African ungulates (e.g. Leuthold & Leuthold, 1978; Irby, 1982; Roberts & Dunbar, 1991; Somer, 1997; Owen-Smith, 1998) and temperate ungulates (Clutton-Brock et al, 1982; Risenhoover, 1986; Houseal & Olson, 1995; Parker et al, 1996), we have a very limited understanding of how ungulates cope with extreme climatic conditions at high latitudes when the time available for feeding in winter is greatly reduced.

We studied the impact of temperature, rainfall and daylength on the activity budgets of feral goats inhabiting the Isle of Rum, a high latitude island off the northwest coast of Scotland. The climate on Rum is wild, wet and windy (Clutton-Brock et al, 1982; Clutton-Brock & Ball, 1987). Ambient temperature (and in particular winter temperature) has been shown to have a significant impact on the population dynamics of the feral goat (*Capra hircus*) population on the Isle of Rum, NW Scotland: stressful winter conditions are probably largely responsible for preventing goat populations in such high latitude habitats from exploding in the way that equivalent populations inhabiting tropical oceanic islands have done (Parks, 1993). This has important implications for habitat conservation if climate warming results in significant increases in ambient temperatures in these high latitude habitats.

Daylength is an important constraint on an individual's behaviour options since it sets the period within which an animal must perform its behaviour (Dunbar, 1988, 1992). Daylength varies greatly with seasons in northern temperate regions, with longer length in summer and a shorter one in winter. Such variation may have important implications for the activity budgets of diurnal animals. Feral goats on Rum are previously reported as diurnal (Gordon et al, 1987; Dunbar et al, 1990; Shi et al, 2003), and thus have to cope with seasonally fluctuating daylength, thereby making the effects of low temperatures on energy balance much worse during winter months.

1 Methods

1.1 Study area and climate

The study was conducted from January 1981 to September 1982, and May to November 2000 (inclusive). The Isle of Rum (57°0′N, 6°20′W) is a small island which is located about 20 km off the northwest coast of Scotland mainland. It measures nearly 14 km from north to south and, at its widest point, approximately 13 km from east to west (Clutton-Brock et al, 1982).

The goats were probably first brought to Rum as

domestic stock some time as early as 1770 s (Dunbar, 1986; Gordon et al, 1987). About 450 inhabitants on Rum were forced to leave for Canada in 1828, and they might have left their domestic goats behind them. These goats may be the ancestors of the current feral goat population on Rum today. The current goat population on Rum is confined almost exclusively to the cliff terraces of the west coast of Rum. The population size has remained relatively stable from 1981 to 2000 with variation from 150 to 200 individuals (Boyd, 1981; Shi, 2003).

Rum has an Atlantic oceanic climate. Temperatures are lowest between December and March with minimum temperatures often below freezing (though rarely by more than a 2 – 3℃). July or August is normally the warmest month. The annual rainfall ranges from 1 800 mm in the coastal zone to 3 000 mm in the hills. The seasonal distribution of rainfall varies substantially between months. Usually, May is the least wet month, though it could be June or even July sometimes. However, each month can be recorded as the wettest of the year. On Rum, the daytime length varies greatly across months with longest average daytime length being about 18 hours in summer months (June & July) and the shortest one about eight hours in December and January.

The high seacliffs (rising 200 – 400 m above sea level) add a significant level of windchill to minimum temperatures: thermometers placed at various locations around the habitat indicated that the cliff tops were typically around 2℃ colder than the beach, and around 4 – 5℃ colder than the beach-level caves in which the goats usually sheltered at night. The effects of windchill are exacerbated by the fact that animals are often soaked by rain: there are on average 200 rainy days a year on Rum. Ground frost is common between October and April, and gales are common during winter months.

1.2 Data collection and analysis

Rainfall and temperature data for Rum were obtained from the Rum NNR long-term records on the Island. The daylength on the 15th day of each month was calculated from the equation available at http://www.qpais.co.uk/modb-iec/dayleng.htm.

Instantaneous scan sampling procedures (Altmann, 1974) were used to collect data on activity budgets between 08:00 and 16:00 in the winter season (shortest observation period) and between 05:00 to 22:00 in summer season (longest observation period). If weather permitted, the activity budget data were collected each day during the study period (no less than 20 days every month). Because it had previously been determined that the feral goats on Rum spent the hours of darkness sleeping/resting in caves or sheltered positions at beach level (Gordon et al, 1987; Shi et al, 2003), only daytime activity budgets are considered in this paper. When sampling, an entire group of goats was rapidly scanned and the behaviour of each individual recorded. Sampling was repeated at 10-min intervals so long as the goats remained in sight.

The main activity categories were classified as follows:

Feeding: biting, chewing, browsing, grazing or swallowing food;

Standing: includes standing still, standing alert and/or standing ruminating;

Lying: sternal recumbence with or without rumination, inclusive of sleeping with eyes closed;

Moving: self-explanatory, including travelling and walking. However, it is overridden by feeding if both occur at the same time.

Time budgets were calculated for each year, each month within each year. Data obtained from all scans were first pooled for each hourly interval. Then, for each hour interval, the activity budgets were calculated by dividing the number of individuals that performed a defined activity by the total number of individuals observed during this interval. This was shown as following:

$$\frac{\sum(\text{records of activity } x)}{\sum(\text{records of all activities})} \times 100$$

These values were then averaged to yield a mean value for the percentage of daytime devoted to each activity for the month in order to avoid biases due to sample size variations (Moncorps et al, 1997). Because previous study (Shi et al, 2003) has demonstrated that feral goats spend most time feeding and lying (over 90% together), this paper emphasizes the influence of climatic factors and daylength on feeding and lying time.

In order to remove the effect of varying daylength across the year (mean daylength at mid-month varied from 7.0 – 18.1 h), the actual number of hours devoted to each activity for the whole daylight period in any given month was calculated by multiplying the mean percentage of the sample day devoted to each activity by daylength for that month. Because foraging is the main daily behavior for feral goats in this study (Shi et al, 2003), and is the most important and dominant be-

haviour in the time budgets of free-ranging ungulates (Clutton-Brock et al, 1982; Bunnell & Gillingham, 1985; Gordon, 1989), we computed the real amount of daytime spent foraging by goats in this paper.

Nonparametric statistics were used for the activity budget data analysis because the percentage data didn't meet the assumptions of parametric procedures and couldn't be appropriately transformed (Sokal & Rohlf, 1995). Regressions were used to determine if there was any influence of mean monthly temperature and monthly rainfall on the time spent in feeding and lying. All statistics were conducted with SPSS (v11.0).

2 Results

Based on the regressions between the climatic variables (mean monthly temperature and rainfall) and the monthly percentage daytime budgets, air temperature had statistically strong negative effects on the proportion of daytime spent in feeding ($r = -0.66$, $F_{1,36} = 23.013$, $P = 0.0002$), but strong positive effects on percentage daytime spent in lying ($r = 0.71$, $F_{1,36} = 42.46$, $P < 0.001$) (Fig. 1). On the other hand, temperature seemed to have no strong effects on standing time ($r = 0.23$, $F_{1,36} = 0.928$, $P = 0.3488$) or on moving time ($r = -0.23$, $F_{1,36} = 0.969$, $P = 0.3385$).

The monthly rainfall didn't have statistically strong influences on the percentage daytime spent in feeding, moving or lying (feeding: $r = -0.096$, $F_{1,36} = 0.517$, $P = 0.475$; moving: $r = 0.232$, $F_{1,36} = 3.138$, $P = 0.082$; lying: $r = 0.208$, $F_{1,36} = 2.494$, $P = 0.120$), but did have a significant positive effect on standing time ($r = 0.378$, $F_{1,36} = 9.175$, $P = 0.004$).

The interactions between temperature and rainfall were detected by partial correlation. The results of partial correlation showed: 1) when the effects of mean temperature were controlled for, monthly rainfall had no significant effects on feeding time ($r = -0.143$, $P = 0.292$) or moving time ($r = 0.256$, $P = 0.085$), but had significant effects on both lying time ($r = -0.304$, $P = 0.023$) and standing time ($r = 0.382$, $P = 0.004$); 2) when the effects of rainfall were controlled, the mean monthly temperature still had significant effects on both feeding and lying time (feeding: $r = -0.696$, $P < 0.001$; lying: $r = 0.766$, $P < 0.001$), but not on standing time ($r = 0.125$, $P = 0.358$) or moving time ($r = -0.093$, $P = 0.496$). This demonstrated that mean temperature may have somewhat obscured the effect of rainfall on lying time, but the interaction effects of temperature and rainfall in this study on other activity budgets were limited.

However, the variable daylength on Rum and the strictly diurnal behaviour of the goats imply that the above analyses may conceal some more complex relationships between temperature and the actual amount of time spent feeding and lying by goats because the seasonal variation in daylength may have important effects on such relationship. We therefore analyzed the effects of air temperature on the actual number of hours spent in feeding and lying by goats. The results are shown in Fig. 2.

It is apparent from Fig. 2 that, partly contrary to the results indicated in Fig. 1, the feral goats increased both feeding time and lying time under higher temperature conditions (feeding: $r = 0.601$, $F = 9.613$, $P = 0.006$, $df = 17$; lying: $r = 0.874$, $F = 55.214$, $P < 0.0001$, $P = 17$). Because the higher temperatures on Rum coincide with the longer daylength in summer months, this result suggests that the daylength in summer is long enough to allow feral goats to spend more time feeding ($r = 0.722$, $F = 18.504$, $P < 0.001$, $df = 17$) as well as lying ($r = 0.930$, $F = 109.080$, $P < 0.001$, $df = 17$).

In order to explore the possible importance of variable daylength in the goats' activity budgets, we computed the monthly real amount of time spent foraging by feral goats in 1981 as described above in the Methods section. The results are shown in Fig. 3.

The real amount of time spent feeding each month by goats was the longest in June and July, and the shortest in December and January (aside from the rutting period in August and September). The longer feeding time in summer months may be partly a direct result of the extended daylength in summer (linear regression, $r = 0.722$, $F = 18.504$, $P < 0.001$, $df = 17$).

This result allows us to discount the possibility that the feral goats on Rum don't need to feed much in warm summer months. In fact, feral goats need to spend as much time feeding as the conditions permit them to, even in summer months. On average, the real feeding time was 7.4 h per day across whole year. If we assume that the goats are in thermoregulatory balance when feeding for the average feeding time (7.4 h), then they are likely to be in serious energy deficit in winter months when they fed less (< 7 h) and the biomass and quality of forage were at the lowest.

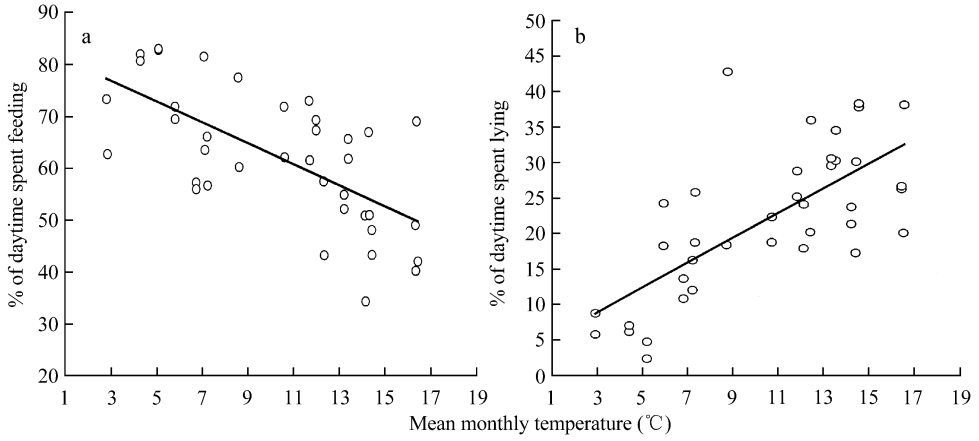

Fig. 1　The relationship between average monthly temperature (℃) and percentage of daytime spent feeding (a) and lying (b) by adult feral goats on Rum in 1981 and 2000

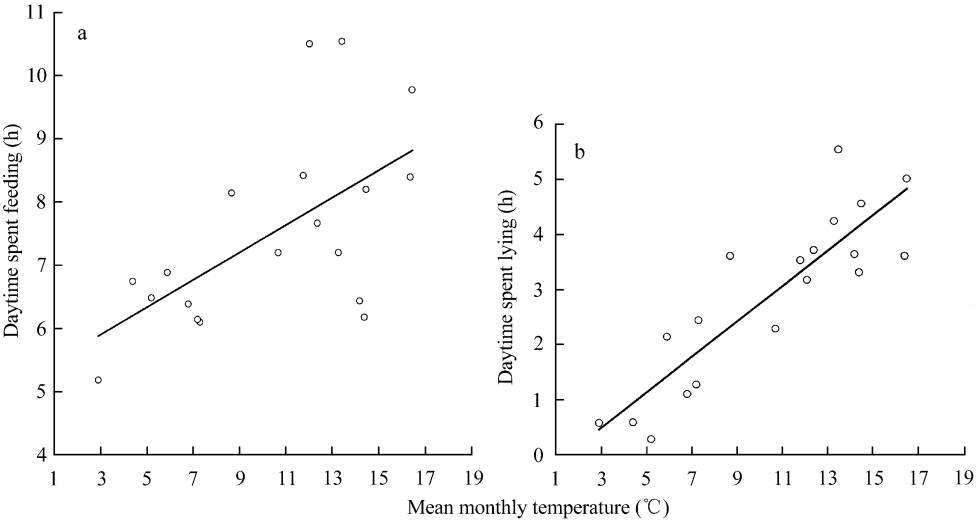

Fig. 2　The relationship between average monthly temperature and the amount of daytime spent feeding (a) and lying (b) by feral goats on Rum in 1981 and 2000

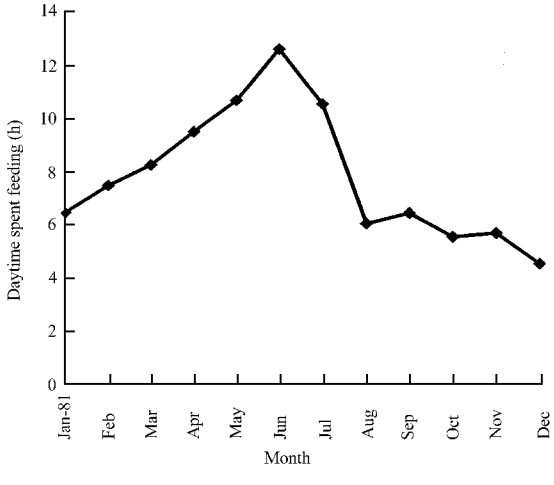

Fig. 3　Mean number of hours per day spent feeding by feral goats on Rum in 1981

3　Discussion

One of the results of this present study showed that there was a significant negative relationship between monthly mean temperature and monthly proportion of daytime spent in feeding, but a significant positive relationship between mean temperature and percentage lying time by feral goats on Rum. However, the real daytime spent in feeding and lying by goats on Rum increased with temperature after the effects of daylength variations were accounted for. Our study also indicates that the feral goats on Rum may still need to feed much even in warm summer months in order to balance their nutrition and energy requirements.

It is reported that higher air temperature tends to depress the proportion of the day that great kudus in

South Africa spend active (Owen-Smith, 1998). For other African savanna animals, extreme high temperatures (>32℃) have also been reported to reduce their activity level (e. g. giraffe *Giraffe camelopardalis*: Leuthold & Leuthold, 1978; impala *Aepyceros melampos*: Klein & Fairall, 1986, etc.). We might anticipate that temperate zone ungulates would have their activity level affected by less because of the lower temperatures prevailing at higher latitudes. Although the activity budgets of elk and deer (*Odocoileus* spp.) are also dramatically reduced during summer months when temperatures are highest (these declined from 70% of the 24-hour day at a mean temperature of 10℃ to about 40% of the day at a mean of 20℃: Belovsky & Slade, 1986), in reality these are as likely to reflect the energy demands of coping with low winter temperatures.

Nicholson & Husband (1992) stated that the feeding behaviour was significantly negatively correlated with temperature, but lying behaviour was positively correlated with temperature for agrimi (*Capra aegagrus*). Pérez-Barbería & Nores (1996) also argued that high temperature might be one of the reasons for the lower grazing time in summer for Cantabrian chamois (*Rupicapra rupicapra*). Similar results are also obtained in other studies. Belovsky & Slade (1986) studied activity budgets of some grassland herbivores (e. g., pronghorn antelope *Antilocapra americana*, bighorn sheep *Ovis canadensis californiana*, and mule deer *Odocoileus hemionus*), and found a significant negative relationship between average daily air temperature and daily activity time.

The increased feeding time for goats during the summer months may thus have less to do with ambient temperature than with increased daylength. The increase in resting time in summer months in this study may also partly reflect the longer daylength because resting time is frequently considered to be reserve of uncommitted time that animals can draw upon when they need to allocate more time to any of the other activities (Dunbar & Sharman, 1984). Nonetheless, the goats may exhibit a trade-off between feeding for longer while they have an opportunity to feed and avoiding heat overload on very sunny days by seeking shelter. On Rum, the goats were observed to be constrained from activity by the relatively high temperatures at midday and early afternoon in July/August presumably in order to avoid the activity-induced thermal loads (Owen-Smith, 1998). During this period, feral goats were often observed moving down to the beach to stay in shelter until late afternoon. In summer months, they tended to start feeding earlier, and then restarted feeding in late afternoon (Shi et al, 2003). Their dense coats presumably make it more difficult for them to keep thermal balance on hot days. As a result, resting time increased on warmer days.

When necessary, feral goats can thus modify their behaviour to cope with higher temperature by starting to feed earlier, and by terminating feeding later and interrupting feeding and seeking shelters in midday. Such behavioural response to environmental changes has also been reported for sheep (Dudzinski & Arnold, 1973) and chamois (Hamr & Czakert, 1986). Baboons also responds to thermal stress both by engaging in more sedentary activities and through seeking shade (Hill, 1999). Based on their own studies on the grassland herbivores and other similar studies, Belvosky & Slade (1986) concluded that activity time appears to be dependent upon thermal balance. This seems to be also the case for feral goats on Rum.

Feral goat time budgets on the Isle of Rum seem to be influenced principally by two environmental factors: daylength and ambient temperature. That feeding time should increase and resting time decrease as temperatures fall comes as no surprise (Clutton-Brock et al, 1982). What is surprising is that time devoted to these activities should also be positively correlated with daylength: the goats fed more in summer months when daylength was longer than they did in winter months when they were under very considerable time pressure because of reduced daylength. Were it the case that the goats were active night and day, this would not be an issue. But, on Rum, the goats spend the night sheltering in caves or other sheltered spots at beach level and did not feed during the hours of darkness. That the Rum goats were prepared to sacrifice foraging time suggests that thermoregulatory costs were a very significant factor. Measurements from min/max thermometers placed at a number of locations within the goats' ranging area suggests that ambient temperatures in the beach level caves were as much as 4℃ warmer than exposed areas on the cliff tops 200 – 400 m above (unpublished data).

These results suggest that the goats might be incurring an enforced energetic cost during winter months. This is confirmed by the fact that estimated energy intake (in terms of forage intake) is significant-

ly lower during winter months than during summer months (Shi et al, 2003). This may in part be driven by the fact that both the biomass and nutritional quality of the goats' food sources may be greatly reduced during winter months (Gordon, 1989). Scarcity of resources, combined with limited daylength, may force the Rum goats to compromise their energy balance and, instead, draw heavily on body fat reserves. The consequences of this shortfall appear to be especially severe for males: male mortality peaks sharply during winter months (Dunbar et al, unpublished). It seems that the goats aim to maximize foraging time during summer months in order to buffer themselves against the energy costs of winter (see also Pickering, 1983). However, males who rut heavily during the late summer may not have sufficient time available for feeding during this period to see them through the winter.

On Rum, both the quality and biomass of most of the plant communities used by goats decreased to their lowest levels in winter (Clutton-Brock et al, 1982; Gordon, 1989). The decreased quality and biomass of forage, combined with the very harsh weather in winter (windchill), may have forced the feral goats to spend as much daytime in feeding as available during the winter months. This was indicated by the high proportion of daytime (> 80%) spent in feeding in January and December (Shi et al, 2003). However, the concurrent decrease in real amount of daytime spent feeding in winter months compared to summer may reflects the limit of daytime available for goats to feed. If there was no such limit, it is reasonable to assume that feral goats should feed much more in winter months than indicated by this study. This suggest that most of the individual goats on Rum might be unable to obtain enough energy and nutrition from foraging in winter months because of the lower quality and biomass of forage and the decreased feeding time. This in turn implies that the feral goats on Rum are malnutrished or in negative thermoregulatory balance, or both, during winter months. Therefore, the seasonal variation in daylength seems to place an upper limit of feeding time for feral goats on Rum, and the availability of active daytime in winter seems to be a limiting factor for feral goats' thermoregulation.

Our study thus highlights the importance of controlling for daylength variations before analyzing and comparing seasonal time budgets for diurnal animals at temperate latitudes. We therefore should interpret with caution those time-budget studies that haven't taken into account daylength variations, especially those studies on northern temperate diurnal animals.

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