CHAPTER 5. Energetic implications

Introduction

In the previous three chapters we have reported on range ecology at important periods in the life cycle of the Porcupine Caribou Herd. We have linked the characteristics of the biophysical environment with the movements, distribution, food habits, and activity of the herd. We have demonstrated that all factors are inextricably linked and that the herd's viability in the long term is probably dependent upon their ability to respond to annual changes in the environment *and* to continue to have the opportunity to exploit key ranges thereafter.

In this section we take our integration one step further by employing computer-assisted simulation modelling to examine the energetic implications of changes in diet and activity budgets for an individual caribou. Recently researchers studying the Porcupine Caribou Herd have formulated a computerized energetics model that tracks the changes in body composition of a caribou throughout the year (Kremsater *et al.* 1989; Hovey *et al.* 1989).

As a group, we have deliberately constructed the model to incorporate much of the data presently available on the herd and its range. The model provides a valuable «bookkeeping service», allowing us, for example, to monitor energy intake over the year, based on our knowledge of feeding times, diet composition and nutrient quality of forage at various stages of phenology. The simulation program allows us to integrate observed changes in diet and activity within and between years, conduct sensitivity analysis to examine which variables contribute most to our estimate of caribou condition, and begin to utilize the model for predictive purposes (e.g. implications of development, climate change).

In this section we have utilized the model to reveal annual trends in activity budgets, diet and energy requirements, to determine how normal changes in these factors affect the energy balance of the individual, to determine if the timing of calving is related to forage variables, and to examine the energetic implications of the strategy of pregnant cows, which migrate earlier than bulls in the spring.

Methods

The model has two compartments, a rumen function submodel that allows the animal to ingest food based on activity budgets, empirical diet and plant community biomasses. Food items are classified into nine plant groups (lichens, evergreen shrubs, etc). The rumen function section then digests the food (on a hourly basis) and updates the three rumen pools (cell wall, cell contents and non-digestible pools). The resultant metabolizable energy intake (MEI) is tallied each day to be utilized by a growth submodel. MEI is allocated within the growth submodel to meet energetic demands of basal maintenance, activity, lactation and/or gestation. If excess energy remains, the animal is allowed to grow (allocated between lean tissue and fat).

After initial simulations we created three data sets for the activity budgets of an adult female; one representing a good year composed of the budgets of winter 1980-81, the late spring/early summer budgets

[1]) The detailed model writeups can be obtained from Environment Canada, Canadian Wildlife Service, Box 6010, Whitehorse, Yukon, Canada Y1A 5L7.

Table 5.1. Fecal fragment density and adjusted diet* (in parentheses) of the Porcupine Caribou Herd in late summer, fall migration and spring migration.

Plant group	Study period		
	Late summer	Fall migration	Spring migration
Graminoids	7.7 (6.9)	3.8 (3.5)	4.0 (4.0)
Lichens	30.0 (39.3)	59.3 (58.0)	16.1 (49.6)
Forbs	0.8 (0.7)	0.8 (0.7)	14.4 (14.4)
Deciduous shrubs	32.7 (29.2)	0.0 (0.0)	0.0 (0.0)
Evergreen shrubs	21.1 (8.1)	9.9 (4.8)	53.6 (20.1)
Mosses	7.7 (6.9)	14.6 (13.3)	11.6 (11.6)
Horsetails	0.0 (0.0)	7.6 (6.9)	0.0 (0.0)
Mushrooms	0.0 (8.9)	0.0 (9.0)	0.0 (0.0)

* Adjusted diet determined from Table 2.17 except that mushrooms were assigned a value of 10% (before normalizing) based on observations of Boertje (1985).

of 1980 and the insect season of 1985; one representing a bad year composed of the winter of 1981-82, late spring early summer of 1979 and the insect season of 1984; and an average year composed of the weighted mean for each period. For the periods not reported previously in this report we used data on activity budgets (Table 5.1) and diet (Table 5.2) collected from limited field work in late summer and fall migration 1989, and from a pellet collection during spring migration (mid April 1987) when migrating females were in the northern Richardson Mountains. This latter sample contained a high component of *Ledum* and relatively low lichens. We conclude that the females are forced to switch to a poorer quality diet earlier than the bulls and non-pregnant cows, which remain back on their lichen-rich wintering areas well into May. We also assumed a spring migration activity budget similar to spring 1980, when animals migrated from winter range early (Table 2.16).

The diet composition used to simulate good, bad and average years for the adult female remained constant and represented the average fecal fragment analyses, corrected for differential disappearance in the form presented earlier (in Winter and Late Spring sections), for each period.

Table 5.2. Activity budgets (%) of the Porcupine Caribou Herd based on 15 minute scans for late summer and fall migration, 1989.

Activity	Study period	
	Late summer	Fall migration
Number of scans	105	10
Number of groups	9	4
Number of animals	7915	47
Feeding (%)	62	52
Lying (%)	14	34
Walking (%)	12	12
Standing (%)	11	02
Running/Trotting (%)	01	00

To examine the energetic implications of spring strategies of bulls versus cows we ran two simulations for each of a single pregnant cow and for a mature bull. We simulated the pattern of metabolizable energy intake, energy balance and weight change for a 160 kg bull if he followed the cows to the calving grounds (i.e. assuming the energy budget and diet reported for the calving grounds) versus if he remained with the bulls on the winter range and migrated north with the rest of the bulls (i.e. assuming activity budgets and diet reported for bulls).

Similarly, we simulated the pattern of metabolizable energy intake, energy balance and weight change for a pregnant female for both scenarios: staying with the bulls or migrating early with the cows.

Results and discussion

Diet – Figure 5.1. illustrates the annual diet of an adult female and male used for the simulations. The figure 5.1. shows the relative importance of lichens to the diet of the Porcupine Caribou Herd over the majority of the year and illustrates the rapid shift in diet in late spring and early summer. These values represent the average diet for the years and periods that we observed. For most periods, diet composition did not vary between years with significantly different amounts of snow and/or insects. Annual variations in diet composition became obvious only from late spring to the movement period. This difference was largely attributable to the timing and pattern of plant phenology and differences in the mobility of the bulls and the pregnant cows.

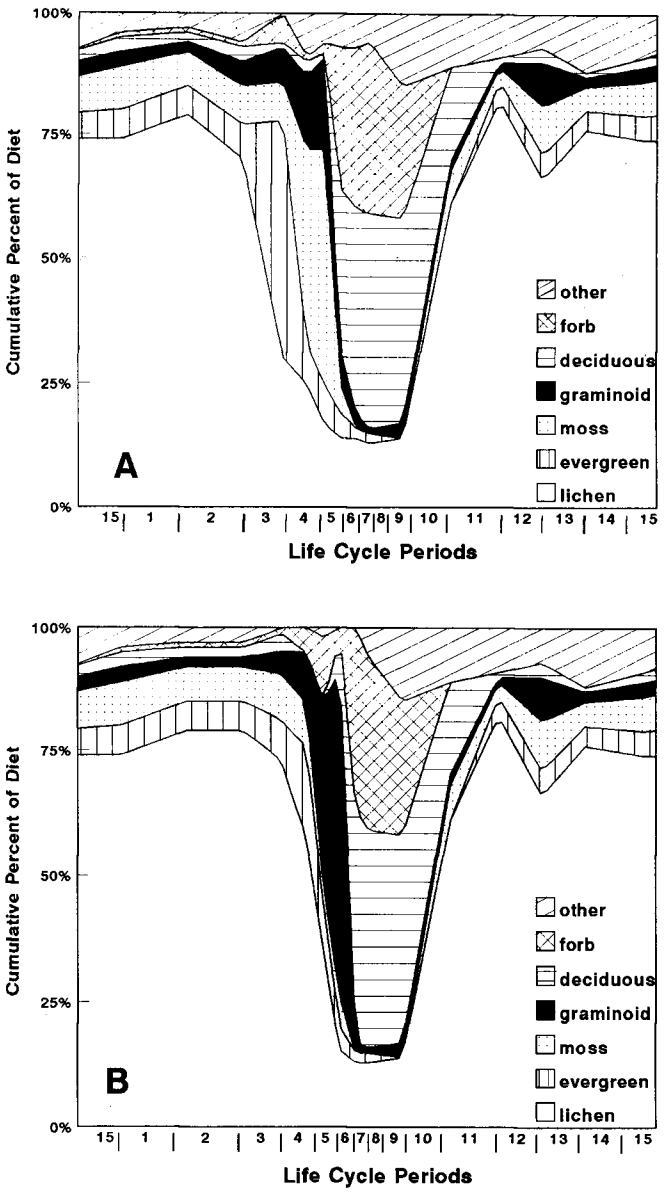


Figure 5.1. Percent of plant groups in the diet of Porcupine caribou adult cow (A) and bull (B). Life cycle periods: 1, mid winter, 2, late winter, 3, spring, 4, spring migration, 5, pre-calving, 6, calving, 7, post-calving, 8, movement, 9, 10, 11, early, mid and late summer, 12, fall-migration, 13, rut, 14, late fall, 15, early winter; dates as in Table 1.1.

Activity budgets – Figure 5.2. and Figure 5.3. presents the annual activity budgets for an adult female (Fig. 5.2A) and bull (Fig. 5.2B) and for an adult female in a «good» versus «bad» year (Fig. 5.3A and 5.3B, respectively) . We observed three distinct peaks in feeding throughout the year; immediately pre-calving, after insect season and again in mid December. There may be some problem with the observed high feeding times in December, because animals may have coincided active cycles with the very limited daylight hours. Thus we may be overestimating percent feeding if we extrapolate our observations to a 24 hour basis. The two other peaks in feeding do however seem predictable; the May peak occurs at the end

of spring migration when animals are on a poor quality diet. Higher feeding times may be associated with the requirement to keep the rumen full while foraging in low biomass habitats. The August peak coincides with the decline in insect harassment. The early December peak and, to a lesser extent, the May peak in feeding came at the expense of walking time while the August feeding peak was at the expense of standing and running. The percent of time spent running and standing only became significant in the insect season and these increases coincided with a decrease in lying time.

During the late winter and spring seasons animals in a «good» year (Fig. 5.3A) have notably shorter lying times and longer feeding and walking times than animals in a «bad» year. «Good» year animals had shorter feeding and lying times and longer standing times in the insect seasons.

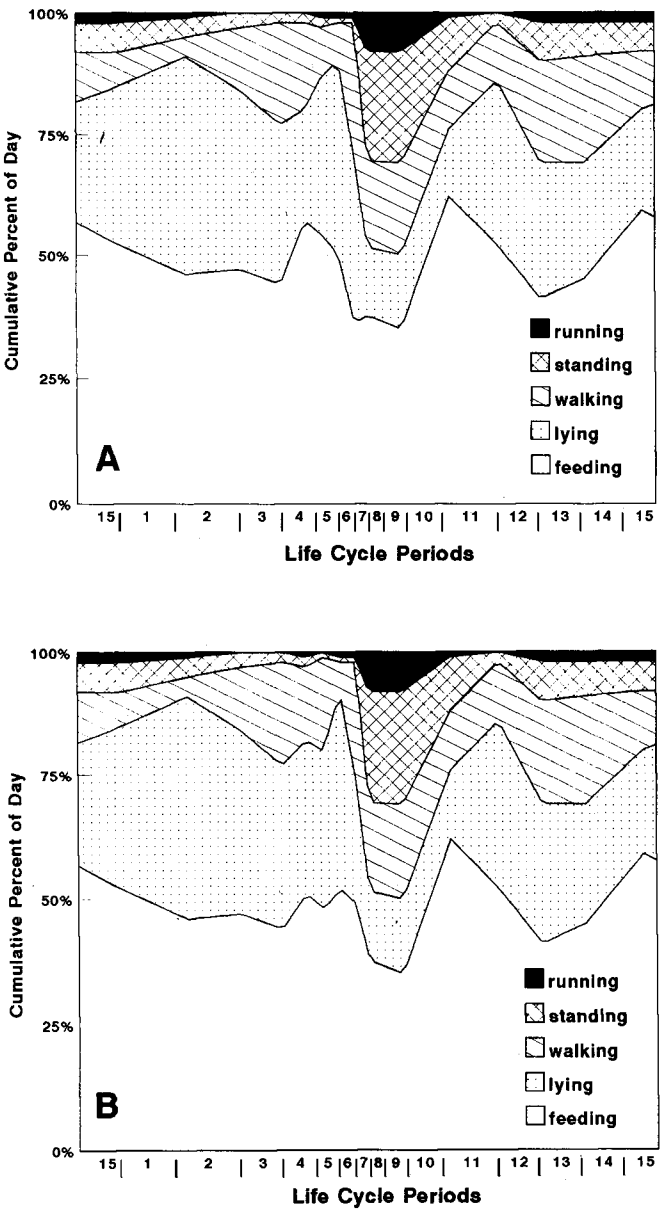


Figure 5.2. Annual activity budgets of an adult cow (A) and bull (B) of the Porcupine Caribou Herd. (Periods as in Fig. 5.1).

Total energy requirements of a lactating/pregnant female in an average year shows a distinct cycle peaking in mid July (Fig. 5.4), coincident with a peak in *metabolizable energy intake* (Fig. 5.5). The timing of calving and thus the timing of lactational demand appears to be highly tuned to phenological changes in the vegetation. In a year of severe insect harassment the MEI peak in July is significantly dampened (Fig. 5.5), as animals reduce the amount of time spent eating. These factors underline the importance of unrestricted movement and ready access to high quality prior to and during the insect season. The critical nature of the late spring/early summer periods cannot be overstated particularly for pregnant and lactating cows. This narrow window of time is critical to the viability of the calf, because it is the period when females are least tolerant to disturbance, when the highest nutrient content of the plants are potentially available and rapidly changing, and when the demands of lactation become the most significant energy expenditure.

The three troughs in metabolizable energy intake (Fig. 5.5) and energy balance (Fig. 5.6) are associated with a combination of poor forage (Fig. 5.7) and reduced intake. In the pre-calving period females

are on a very poor diet. They have left the lichen-rich boreal forest in the south and arrive at the calving grounds prior, in most years, to new flushing vegetation.

Another trough in metabolizable energy intake occurs in August. Lactational demands are still relatively high at the same time that forage quality is rapidly declining due to plant senescence. The final trough in metabolizable energy intake occurs at the rut as a result of decreased feeding times. Pregnant and lactating cows can be in a negative energy balance from spring migration to fall migration in a year of late snowmelt and severe insect harassment («bad» year, Fig. 5.6).

Another parameter that we can use to monitor forage quality is the mean *digestibility* of the diet (Fig. 5.7). The pattern is similar to the MEI cycle, with cows on the poorest range (in terms of digestibility) in late spring and on best range by late June. Therefore, animals experience the lowest mean digestibility at the peak of calving and the highest mean digestibility at the time of peak lactational demand. The subsequent gradual decline in mean digestibility corresponds to declining forage quality. Such is not the case for the bulls that can track plants in early phenological development throughout the spring to pre-calving period and enjoy higher digestibilities than the cow (Fig. 5.7).

The integration of all these parameters to an individual caribou is tracked through the pattern of *fat change* throughout the year (Fig. 5.8). For the simulations of good and bad years we can see a wide divergence in the pattern and amount of fat. In good winters our data suggests that the animals can deposit fat until early spring and throughout the insect season. In poor years fat is lost during both winter and the insect season.

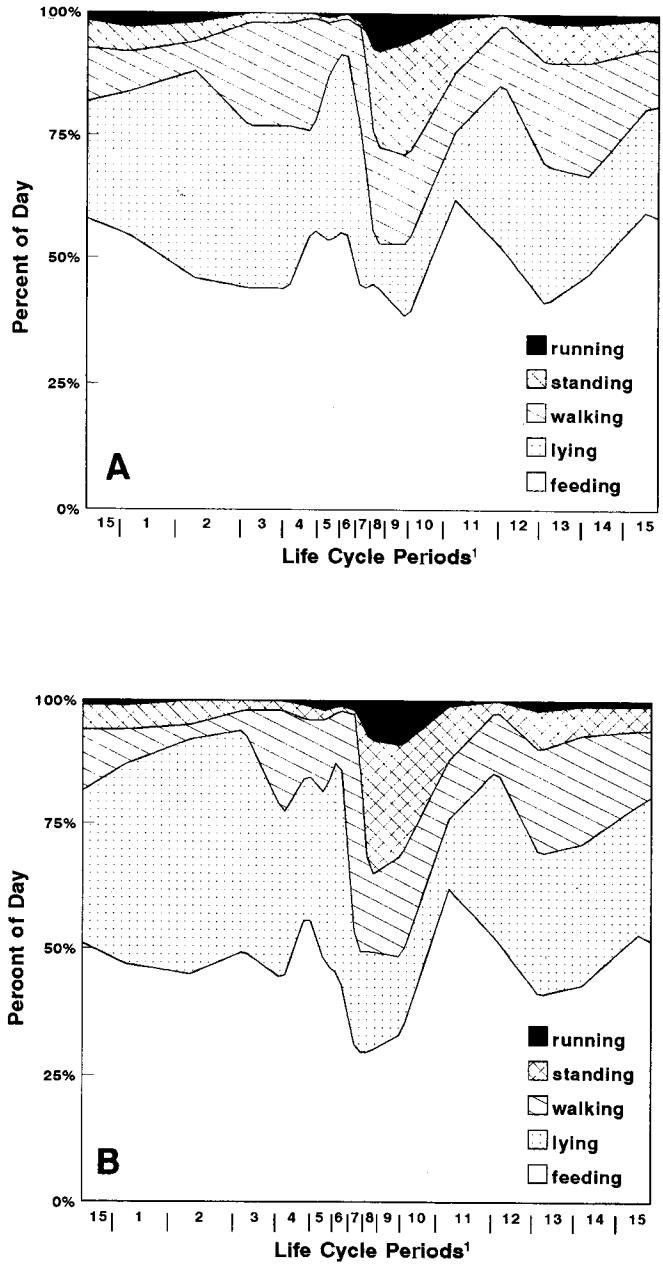


Figure 5.3. Annual activity budgets of a Porcupine caribou adult cow in a «good» (A) versus «bad» year. (Periods as in Fig. 5.1.)

If we look at average daily (Fig 5.9A) and total seasonal (Fig 5.9B) *fat change* change, in relation to our 15 time periods, we see that the greatest daily weight loss is in the calving period, largely as a result of high late gestational and early lactational costs and low forage biomass. Cows can then regain weight in the movement and early summer prior to insects becoming the major disruptive factor to food intake and prior to plant senescence. Fall migration is an important period in terms of replenishing fat

reserves. From our simulations animals can gain fat throughout the winter seasons in an average year, although if our estimate of percent feeding in early winter is high, then the high fat gain values may be overestimated.

One of the values of the simulation models is that it allows us to assess energetically the strategies employed by caribou. In this section we discuss the energetic implications of the strategy employed by bulls versus pregnant cows at the critical time of year (1 April to 30 June). Bulls remain longer on the winter range, migrating north about three weeks later than the pregnant cows. They are thus better able than cows to track vegetation phenology in the pre-calving and calving period. Cows arrive on the calving grounds prior to initial new growth of the forage species.

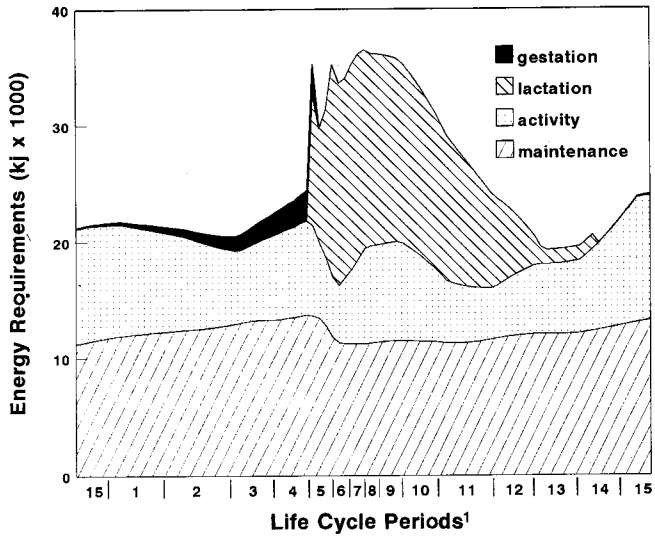


Figure 5.4. Total seasonal energy requirements of an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

The larger body size of the bulls imposes a higher energy requirement than smaller-bodied cows. Therefore, even with the added costs of gestation, energy requirements of bulls remain higher than cows until after calving, when the reverse situation occurs (Fig. 5.10). In fact, when the energy requirements of lactating females are beginning to peak, bull requirements begin to decline (Fig. 5.10). By remaining on the winter range longer, bulls can better meet their higher basal energy requirements. For the two bull scenarios, we can see that the bull remaining back and tracking phenology into late May is in a much more favourable energy balance than a bull migrating early with the cows (Fig. 5.11). It is only after calving that this latter bull gains some energetic advantage (Fig. 5.12). However, on average, the bull which remains with the bulls enters the insect season in slightly better shape compared to if he migrated early with the pregnant cows (Fig. 5.12).

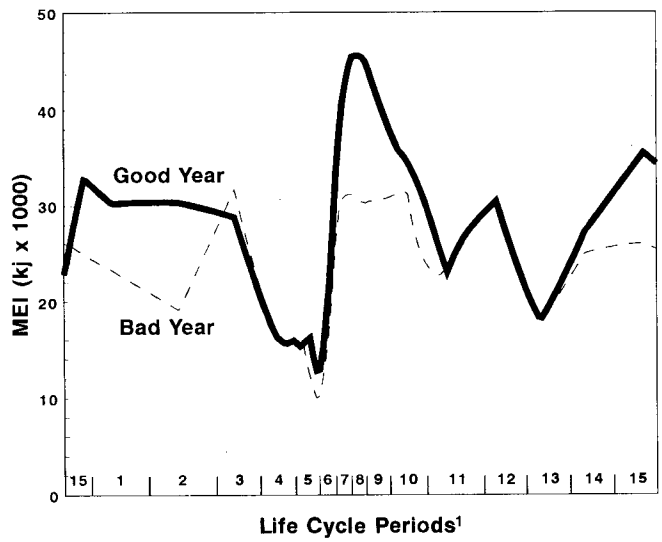


Figure 5.5. Metabolizable energy intake (MEI) – «good» year versus «bad» year for an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

Because the cow has a lower basal metabolic demand, she is able to cope better with the poorer quality spring forage encountered north of treeline than could a bull. If a pregnant cow remained with the

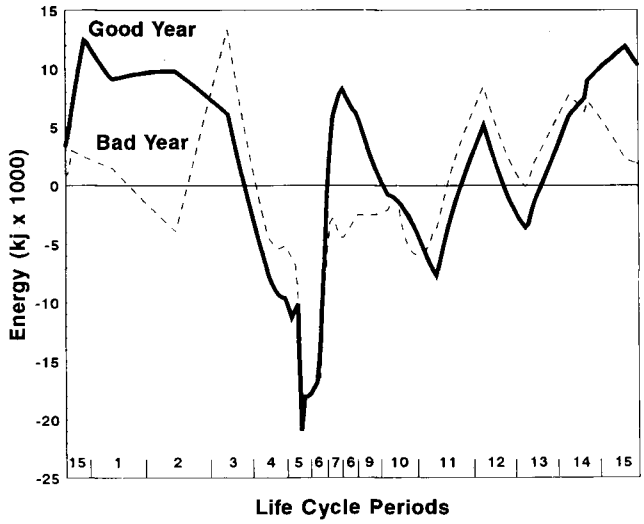


Figure 5.6. Energy balance – «good year» versus «bad» year for an adult cow of the Porcupine Caribou Herd. (Periods as in Fig. 5.1.).

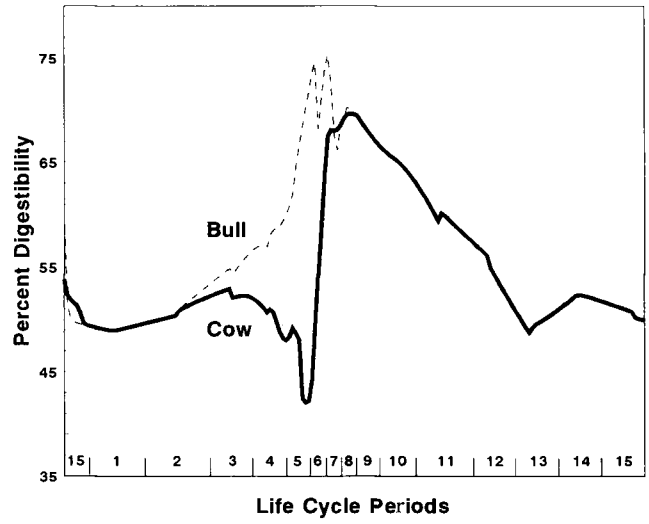


Figure 5.7. Seasonal digestibility of the diets of an adult cow and bull of the Porcupine Caribou Herd. (Periods as in Fig. 5.1.).

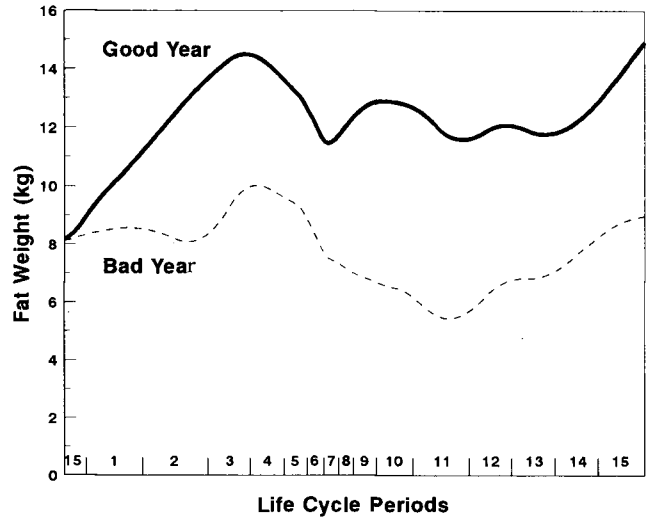
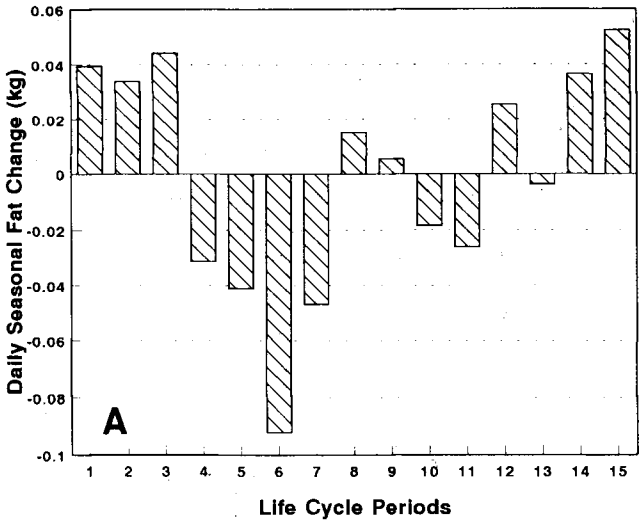


Figure 5.8. Weight of body fat reserves of a female Porcupine caribou in a «good» year versus «bad» year. (Periods as in Fig. 5.1.).



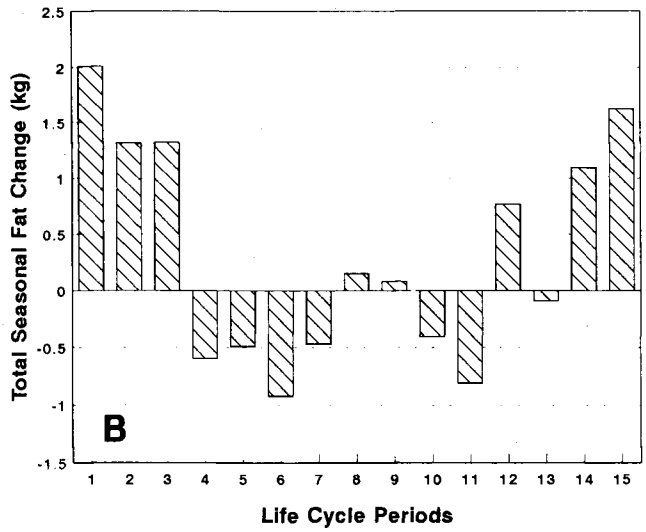


Figure 5.9. Average daily (A) and total (B) seasonal fat change for an adult female Porcupine caribou. (Periods as in Fig. 5.1.).

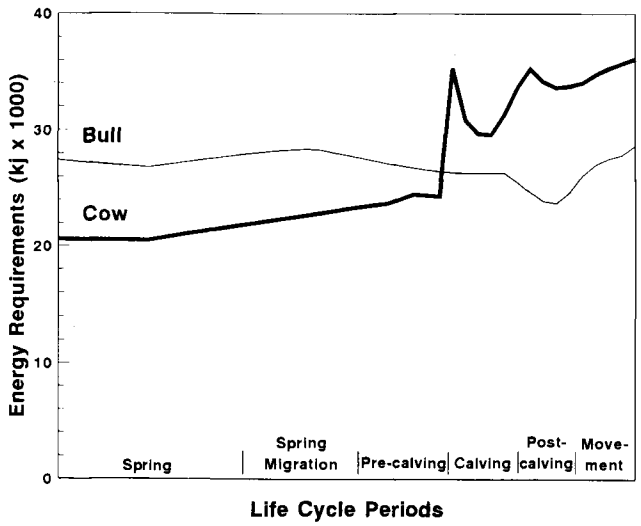


Figure 5.10. Total energy requirements for a bull and cow from the Porcupine Caribou Herd, from spring to the movement period. (Periods as in Fig. 5.1.).

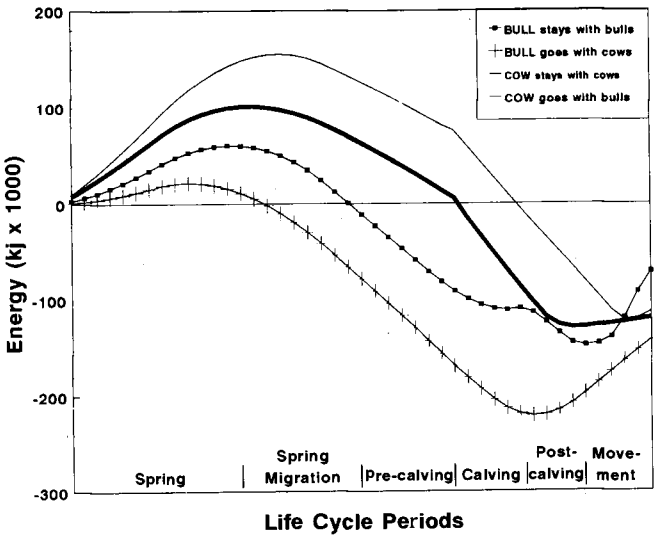


Figure 5.11. Cumulative energy balance for four simulated scenarios: bull staying with bulls; bull going to calving grounds with cow; cow staying with cows; and cow remaining on winter range with bulls, tracking early spring phenology.

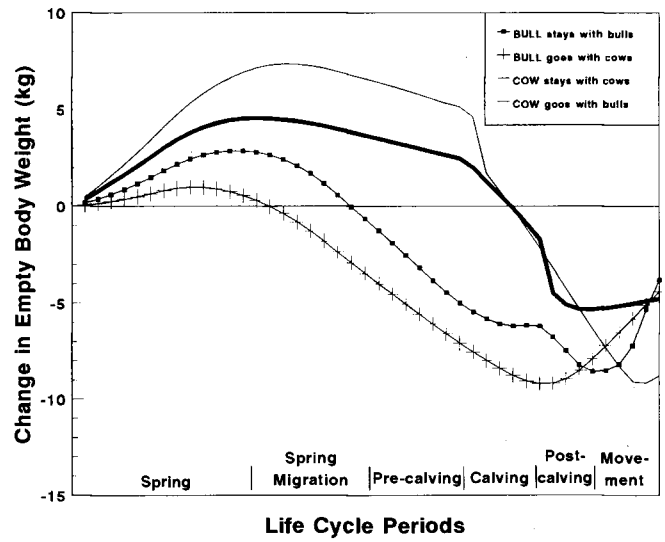


Figure 5.12 Empty body weight of bull and cow Porcupine caribou under four simulated scenarios: bull staying with bulls; bull going to calving grounds with cow; cow staying with cows; and cow remaining on winter range with bulls, tracking early spring phenology.

bulls she would gain a energetic advantage until calving. As soon as lactational demands become significant the cows on the calving ground gain the energetic advantage (Fig. 5.11). The difference in the month of June is so significant that the cows moving early to the calving ground enter the insect season in significantly better shape than if they followed the strategy of the bulls (Fig. 5.12).