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ECOLOGICAL AND PHYSIOLOGICAL ASPECTS OF CARIBOU ACTIVITY AND RESPONSES TO AIRCRAFT OVERFLIGHTS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements of

DOCTOR OF PHILOSOPHY

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ABSTRACT

I investigated the use of remote-sensing of caribou (Rangifer tarandus) activity to assess disturbance of low-altitude overflights by jet aircraft. Resource management agencies are concerned about the potential effects of these overflights on important species of ungulates. I hypothesized that low-altitude overflights would affect activity and movements of caribou, and thereby constitute a disturbance with negative consequences on energetics. I used caribou of the Delta Herd (DCH) and captive animals at the Large Animal Research Station (LARS) to address the hypotheses: caribou (1) exhibit equal activity day and night; (2) do not time activity to light; and (3) activity patterns do not change seasonally in response to daylength. Caribou were nychthemeral and exhibited uniform activity with no apparent timing to light. DCH caribou responded to seasonal changes in the environment by modifying activity (increased activity in response to insect harassment), whereas LARS caribou altered activity in response to fluctuating physiological variables (increased activity during rut). Changes in daylength did not affect activity. Data on activity from LARS and DCH caribou were compared with extant data on caribou of the Denali and Porcupine herds. Poor quality forage in winter was inferred from long resting bouts, and low availability of forage was inferred from long active bouts of post-calving caribou of the DCH. In midsummer, caribou of the DCH exhibited significantly longer active and shorter resting bouts than did LARS caribou, consistent with a moderate level of insect harassment. Responses of caribou to overflights were mild in late winter and, thus, overflights did not constitute a disturbance. Post-calving caribou responded to overflights by increasing daily activity, linear movements, incremental energy cost, and average daily metabolic rate. Energetic responses and movements were significantly related to the loudest overflight of the day. In the insect season, activity levels increased significantly in response to overflights but with no corresponding increase in linear movements or energetics. My recommendations are to prohibit aircraft overflights of caribou during calving and post-calving periods and during key feeding times in insect harassment seasons. Research indicates the possibility of more severe effects in nutritionally stressed animals.

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DEDICATION

To Chandalar, Romanzof, Delta, Barter, Thelon, Brochet, Windflower, Hula Hula, Malcolm, Paddockwood, 007, Gentian, Kiska, and Tuktoy.

Also Gumbie, Ptar, Pokok, Brooks, Pingo, and Jasmine.

They gave all so that we may learn.

INTRODUCTION

This thesis addresses the use of remote-sensing of animal activity for assessment of disturbance by overflights of low-flying jet aircraft on caribou (Rangifer tarandus). I hypothesized that low-altitude overflights by military jet aircraft would affect both daily activity patterns and movements of caribou, thereby constituting a disturbance that would have negative consequences on energetics. A literature search showed that responses of animals to anthropogenic events may be related to the evolved response of animals to predators, and based on stochastic ecological factors. To interpret the responses of caribou to jet overflights, I needed to improve my understanding of basic activity patterns of caribou. Thus, I collected activity data on captive caribou that were undisturbed at the Large Animal Research Station (LARS), which were free-ranging in 10 ha fields but not subjected to energetically costly factors such as food deprivation, insect harassment, predation, and deep snow. These data were contrasted with data from wild caribou of the Delta Caribou Herd (DCH) in interior Alaska. Given that caribou are a gregarious species with well-defined, within-group synchrony of activity and a predator-avoidance strategy based on swamping of predators (during calving) and group vigilance (during other seasons), I reasoned that there was an adaptive advantage to foraging throughout a 24-h period and no advantage in timing of activity to light or photoperiod. I hypothesized, therefore, that caribou would exhibit equal activity day and night, that caribou would not time activity to sunrise or sunset, and that seasonal changes in activity would not occur as a consequence of photoperiod. As such, innate changes in activity would occur seasonally, in response to reproduction. On the other hand, innate rhythms can be modified as animals respond to environmental factors, including nutrition, weather, and predation, most of which are stochastic. Because nutritional status was considered an important factor affecting activity, the nutritional status of the study herd (DCH) was estimated. Finally, the energetic consequences of behavioral responses of caribou to overflights by jet aircraft are addressed by assigning an energy cost (the incremental energy cost [IEC]; Fancy and White 1985) to the main activities of caribou.

The U. S. military has conducted training exercises in Alaska for > 30 years. These training exercises have increased in number by 30% since 1990 because of the reduction of military bases overseas and the limited area available in the continental 48 states (U. S. Air Force, Pacific Air Force, 1995). The general public and resource management agencies are concerned about potential effects of these training exercises on important species of ungulates, such as caribou and moose (Alces alces). Accordingly, the U. S. Air Force initiated studies to investigate responses of ungulates to disturbance by military jet aircraft, and this study was developed to specifically assess effects on caribou. To improve our assessment, basic information on the inherent patterns of activity of caribou was needed; this information is addressed in Chapters 1 and 2. The issue of the effects of low-altitude overflights by military jet aircraft on activity and movements is detailed in Chapter 3, and energetic consequences of such overflights are evaluated in Chapter 4.

The DCH, of interior Alaska, was chosen for study because of its proximity to Eielson Air Force Base and Fairbanks, Alaska. The range of this herd is the northern foothills of the central Alaska Range, approximately 60 km south of Fairbanks (Chapter 3, Fig. 18). The herd has exhibited relatively dramatic fluctuations in size over the past 25 years, because of heavy harvest by humans, predation, and recently, nutritional constraints (Davis et al. 1985, Valkenburg 1993, 1994). The herd maintained an apparently stable number between 5,000 and 6,000 animals during the early 1970s, but declined to a low of 2,500 animals about 1975. This decline was ascribed to heavy harvest by hunters and wolf predation on calves (Davis et al. 1985). The herd rebounded following a program of wolf reduction instituted in 1976, increasing to more than 7,000 caribou by 1982. The population size of the DCH was estimated to be 10,900 in 1989. From this time, however, the herd has been in a period of decline, reaching a low of 3,600 animals in 1993, despite the cessation of human harvest in 1990. A program of wolf reduction again was initiated in 1994. Evidence that the DCH exceeded carrying capacity also is important to the interpretation of population trends. Depleted lichens on winter range has been identified based on a low proportion of lichen in fecal pellets, a correspondingly high proportion of moss in the diet (Valkenburg 1994), and abandonment of the traditional wintering (Fleischman 1990) and calving grounds. In addition, the population has suffered lowered calf survival, decreased growth rates of calves to 10-months-of-age, and a delay in age at first reproduction. These latter findings suggest a decline in quality of summer as well as winter range.

By comparing activity patterns of the DCH with activity of caribou herds of known nutritional planes, I hypothesized that I could deduce if the DCH was limited nutritionally during this study. Captive caribou at LARS were used to collect baseline data on activity and to gain an impression of the evolutionary history and life-history strategies that determine activity patterns. Measurement of the activity of caribou of the DCH during disturbance by military aircraft therefore is extrapolated to an estimate of long-term effects of disturbance by jet aircraft on this ungulate species. The DCH has been described as “the most highly disturbed herd in Alaska” (Davis et al. 1985), but at that time (i.e., early 1980s) the herd showed no adverse effects on reproduction or on the population. Interpretation of these results must be tempered by the knowledge that this herd could be nutritionally stressed in more recent times (Chapter 2). Moreover, the energetic consequences of overflights to a group of animals that already is nutritionally challenged, may have important implications for the reproductive success of female caribou (Chapter 4), thereby constituting a measurable negative effect.

Activity patterns of ungulates ultimately are determined by environmental factors including quality, availability, and distribution of resources, predation, competition, and weather (Wilson 1975). Consequently, nocturnal, diurnal, nychthemeral, and crepuscular patterns of activity have evolved. Individuals exhibiting these patterns are equipped to exploit particular temporal and spatial niches. Processes of foregut and hindgut digestion not only allow animals to exploit food niches, they also may allow maximization of food storage or digestion when animals must rest or hide for extended periods. In situations of low availability of resources, maximizing food intake may underpin activity. Ruminants can maximize intake of digestible energy through regular feeding and rumination bouts, which in the extreme, are expressed as equal activity day and night (nychthemeral) (Leuthold 1977). Thus, the way in which animals react to anthropogenic events and overflights, in particular, could be controlled by these evolved and ecological factors.

The ability to time the initiation of feeding and other activity enables animals, living in a variable environment, to anticipate predictable environmental characteristics that occur at specific intervals, or in daily rhythms (Alcock 1989). Ruminants would benefit from the ability to time activity, regardless of which activity pattern they exhibit. For example, timing activity may enable animals to exploit dew water in dry environments, exploit diurnal changes in food quality, and to feed in the cool of the day, thereby, avoiding high daytime temperatures (Daly et al. 1992, Hughes et al. 1995). Timing of activity could facilitate group foraging, and synchrony of activity, thus, effecting predator avoidance through group vigilance (Estes 1974, Berger et al. 1983, Skogland 1984). The mechanism by which activity is timed likely because of internal rhythms that may be entrained by predictable environmental cues or *Zeitgebers* (Aschoff 1960), including photoperiod (Pittendrigh and Minis 1964, Menaker 1969, Krüll et al. 1985). The extent to which an advantage can be achieved by timing of daily activity has a strong seasonal component, especially to cue reproduction and migration.

Caribou are social ungulates existing in extreme seasonal environments, which result in seasonal changes in forage availability and quality, physiological needs, and predation by mammals and parasitism by insects. Forage quality and availability impose a daily influence on activity patterns that change in a seasonally distinct pattern. Weather events are more stochastic and, therefore, may predominantly influence daily activities in winter (Skogland 1984, Post 1995). The influence of predation in timing of activity has both intrinsic and stochastic components. Social foraging (Berger et al. 1983, Molvar and Bowyer 1994) and habitat selection (Sinclair and Arcese 1995) are important consequences of predation. Each of these components (forage quality, forage availability, predation, insect harassment, weather) may, at a given time, be the primary determinant of apparent patterns of activity. Insect harassment, for example, results in a decrease in the time spent feeding and, thus, overrides the intrinsic feeding rhythms normally exhibited by caribou (White et al. 1975, Dau 1986, Murphy and Curatolo 1987, Nixon 1991, Russell et al. 1993).

Effects of an unusual or anthropogenic disturbance on daily patterns of activity are likely determined by the way in which the disturbance mimics one that is more natural. For example, human forms may resemble bear or other predators and artificial sounds or winds may mimic effects of insects. For caribou, natural disturbances, such as predation by mammals or harassment by insects, result in decreased lying and foraging and increased movement (White et al. 1975, Russell et al. 1993). Anthropogenic disturbances too are known to affect caribou by increasing activity at the expense of lying (Murphy and Curatolo 1987, Murphy et al. 1993). Therefore, measuring patterns of activity of caribou could be used to gain an understanding of whether anthropogenic activities, which are potentially disturbing, could constitute a significant disturbance.

Evidence that jet overflights harass caribou and, thereby, constitute a disturbance may well depend on the ability of individuals and the population to accommodate to any changes of activity attributable to the aircraft. Small changes in time taken from grazing combined with reduced time available for food digestion, consequences of general anthropogenic effects on caribou, can have multiplicative effects on energy balance of caribou (White 1983). Recent evidence for Arctic herds show that caribou have a limited ability to compensate to environmental stress when they are exhibiting density-dependent effects (Cameron et al. 1993, Cameron and VerHoef 1994). The consequence of these combined effects is a decline in reproduction because of nutritional effects acting on body weight and fatness (Reimers 1983, Cameron et al. 1993, Cameron and VerHoef 1994, Gerhart 1995). Therefore, I considered it necessary to determine if the DCH could be compromised by range conditions in its response to single and repeated overflights by jet aircraft.

This thesis comprises four chapters, each of which represents a separate manuscript to be submitted for publication to professional journals. Consequently, each chapter retains its original author designations (as a footnote to the title page of each chapter), abstract, introduction, and conclusion. References are consolidated into a single section at the end of the thesis. I collaborated with Stephen M. Murphy in a portion of this research, but wrote the thesis myself, except the noise-exposure sections in Chapter 3. Robert G. White and Stephen M. Murphy initiated the research regarding effects of overflights by low-flying military jet aircraft on activity of caribou. Nevertheless, I designed the portion of the research utilizing Wildlink radiocollars to measure daily responses of caribou to overflights. Robert G. White contributed to the inception of the study and the development of the research design. Each chapter addresses a discrete aspect of activity or energetics of caribou. Chapter 1 addresses environmental influences on the timing and synchrony of activity in caribou. Chapter 2 evaluates the effects of ecological factors on activity cycles. Chapter 3 discusses the effects of overflights by low-altitude jet aircraft on caribou activity and movement. Finally, Chapter 4 assesses the energetic consequences of overflights on caribou. The overall study and recommendations for management are detailed in a Synopsis.

CHAPTER 1: TIMING AND SYNCHRONY OF ACTIVITY IN CARIBOU[1]

Abstract: Barren-ground caribou (Rangifer tarandus granti) purportedly are primarily diurnal animals with principal activity occurring at sunrise and sunset. Activity patterns are a response to available food, particularly because caribou persist in an open, relatively homogenous environment, with highly gregarious foraging activities, and utilize the confusion effect as a predator-avoidance strategy to minimize predation risk of individuals. We hypothesize that these characteristics should typify an activity strategy whereby caribou are active equally day and night, which we term "nychthemeral" activity, with no requirement for crepuscularity. To test this hypothesis, we investigated the activity patterns of 2 caribou populations: one captive and the other wild and free-ranging in the northern foothills of the Alaska Range in interior Alaska. We collected data on 24-h activity using focal-animal behavioral sampling on captive caribou and activity-monitoring radiocollars (Wildlink, Inc.) on wild caribou. Caribou of both populations exhibited equal activity day and night (nychthemeral activity) and did not time daily activity to sunrise or sunset. Wild caribou exhibited no between-group synchrony. In contrast, within-group synchrony of activity was high in both herds in all seasons. We conclude that activity patterns of caribou are driven primarily by their need to balance feeding and resting-rumination in continual cycles to ensure maximum food intake and efficient digestion. Differences were observed between wild and captive caribou and were attributed to ecological factors that could constitute time and energy costs of living in the wild. We suggest that activity patterns can be used as a diagnostic tool to evaluate ecological influences on caribou populations. Seasonal environmental influences, particularly those that affect forage availability and quality and those related to insects and mammalian predators, had a modifying influence that can lead to a preponderance of daytime feeding activity, sometimes timed to sunrise.

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Key words: activity, diurnal, caribou, crepuscular, nychthemeral, predation, Rangifer tarandus, synchrony, timing.

Introduction

Activity patterns of herbivores are driven by daily requirements, including maintenance, growth, and reproduction (Horn and Rubenstein 1984) and are subject to seasonal changes in biotic (forage quality, forage availability, insect harassment) and abiotic (temperature, precipitation, and wind) factors. Thus, nocturnal, diurnal, nychthemeral, and crepuscular patterns of activity are behavioral expressions of the way animals exploit particular temporal and spatial niches. We defined activity patterns as specific and mutually-exclusive strategies to avoid confusion when contemplating ecological pressures driving the evolution and present-day fitness of individual species of ungulates. Thus, diurnal activity is defined as activity that occurs primarily during the day, nocturnal activity is activity that occurs mostly at night, crepuscular activity is concentrated during twilight (sunrise and sunset), and nychthemeral activity occurs across the entire 24-h period. Although these strategies are mutually-exclusive, animals engaging in these strategies may time their activity to sunrise (Fig. 1).

Animals that engage in nocturnal activity may avoid diurnal predators (Daly et al. 1992, Hughes et al. 1994), although they then are susceptible to predation from nocturnal ones. Additionally, nocturnal activity occurs commonly in animals living in desert environments suggesting an added adaptation to avoid high daytime temperatures. Animals that exhibit diurnal activity not only have opportunities offered by daylight foraging but also are adapted to avoid predators that are also diurnal. Moreover, diurnal patterns of activity may evolve to secure temporal separation between diurnal and nocturnal competitors existing within a common spatial and similar ecological niche (Hughes et al. 1994). We hypothesize that nychthemeral activity may be an adaptation that maximizes feeding efficiency in ruminants. Regular feeding plays a critical role in stabilizing the environment of microorganisms in the rumen, which in turn maximizes digestive efficiency (Leuthold 1977, van de Veen 1979, Kay and Staines 1981). Activity patterns, reminiscent of nychthemeral activity, have been documented in impala

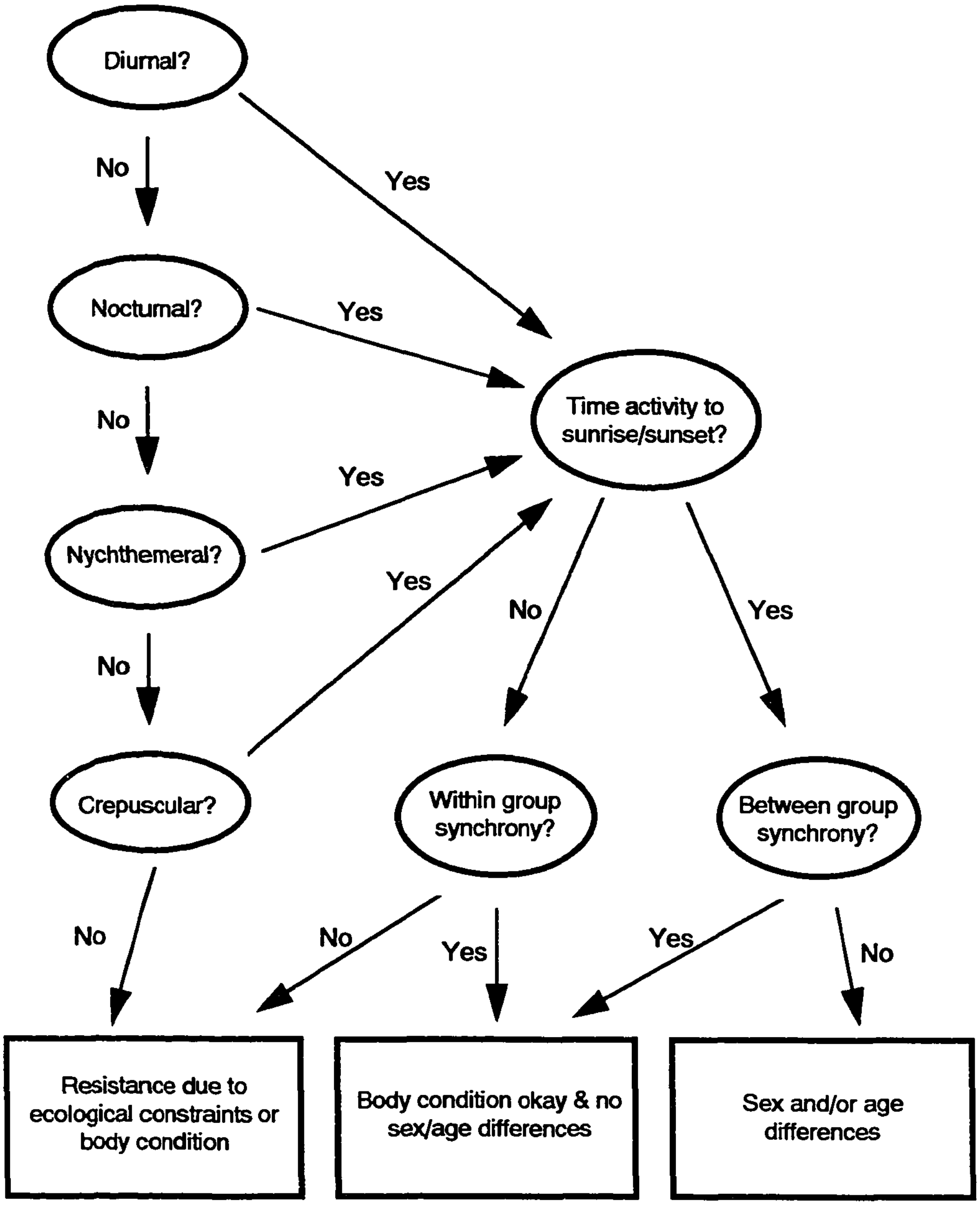

Fig. 1 Conceptual model of ecological and physiological aspects of activity of caribou.

(Aepyceros melampus) (Jarman and Jarman 1973), Thomson's gazelle (Gazella thomsoni) (Walther 1973), wildebeest (Connochaetes taurinus) (Berry et al. 1982), moose (Alces alces) (Risenhoover 1986, Cederlund 1989, Van Ballenberghe and Miquelle 1990), roe deer (Capreolus capreolus) (Cederlund 1989), and reindeer (Rangifer tarandus) (Eriksson et al. 1981, Collins and Smith 1989). Nonetheless, these authors refer to these ruminant species as "primarily diurnal," despite the incidence of activity throughout the 24-h period (Eriksson et al. 1981, Berry et al. 1982, Collins and Smith 1989). The distinction among diurnal, nocturnal, crepuscular, and nychthemeral patterns of activity reflects clearly disparate ecological pressures and physiological requirements.

In some rodents, such as kangaroo rats (Dipodomys merriami), crepuscular activity occurs in response to predation (Daly et al. 1992). The phenomenon is likely a general response to predation. Other factors such as forage quality may be implicated too because a wide range of species exhibit crepuscular activity, including: white-tailed deer (Odocoileus virginianus) (Kammermeyer and Marchinton 1977, Beier and McCullough 1990), mule deer (O. hemionus) (Mackie 1970, Eberhardt et al. 1984, Relyea and Demarais 1994), Roosevelt elk (Cervus elaphus) (Bowyer 1981), red deer (C. elaphus L.) (Bubenik and Bubenikova 1967, Butzler 1974, Georgii 1981, Georgii and Schroder 1983), caribou (Rangifer tarandus) (Roby 1978, Russell et al. 1993), reindeer (Eriksson et al. 1981, Collins and Smith 1989), moose and roe deer (Cederlund 1989). Predators, likewise, are known to be crepuscular (Larivière et al. 1994), conceivably a response to the crepuscular behavior of their prey. Species of rodents that are typically nocturnal commonly engage in crepuscular activity on nights when there is a full moon (Daly et al. 1992), demonstrating a flexibility that necessarily exists in the foraging strategies of many species.

Timing of activity to light may occur concurrently with each of the activity strategies discussed previously (i.e., nocturnal, diurnal, nychthemeral, and crepuscular activity) and, thus, is not unequivocally related to any one of them (Fig. 1). The ability to time activity enables an organism to anticipate predictable environmental characteristics that occur at specific intervals and corrects intrinsic patterns of rhythmicity (Alcock 1989). Sunrise, sunset, and photoperiod constitute the most reliable cues or *Zeitgeber* (Aschoff 1960, Pittendrigh and Minis 1964, Menaker 1969, Krüll et al. 1985). Many species of animals living at mid- and high-latitudes use changes in photoperiod to regulate the temporal pattern of daily and seasonal events (Krüll et al. 1985, Alcock 1989).

Timing of activity to light should lead to synchrony between individuals (Gerkema et al. 1993) or between groups, in the instance of social animals (Fig. 1). Clearly, between-group synchrony would be expected if all animals (or groups) begin daily activity at the same light level (Gerkema et al. 1993) even when the individuals or groups are geographically separated. Between-group synchrony could break down, even if all animals begin activity simultaneously, if different age and sex classes forage differently (White et al. 1975, Leuthold 1977, Engen and Stenseth 1989, Illius and Gordon 1990, Forchhammer and Boomsma 1995). Other factors that could result in a lack of synchrony include situations when animals of disparate groups are subjected to forage of dissimilar quality or availability (Post 1995), or if discrepancies exist in body condition between animals, which results in an attempt to compensate for poor condition through increased foraging (Gaare et al. 1975, Boertje 1981, Cameron and White, in prep). Within-group synchrony, independent of the population, is a by product of social foraging, ultimately caused by enhanced reproductive success (Alexander 1974, Jarman 1974, Pyke et al. 1977, Caraco 1979a, b) through increased foraging efficiency and predator avoidance (Berger et al. 1983) and, likely, is not related to photoperiod *per se*.

Our objectives were to: (1) measure 24-h patterns of activity of wild, free-ranging caribou of the Delta herd in each of 3 seasons: late winter, post-calving, and the summer-insect season; (2) measure 24-h patterns of activity of captive caribou year-round; (3) determine the extent to which caribou (wild and captive) time activity to sunrise; and (4) determine the extent of within- and between-group synchrony in captive and wild caribou, respectively. We collected data to test the following null hypotheses: (1) caribou exhibit activity equally day and night; (2) there are no seasonal differences in number of activity cycles of wild and captive caribou; (3) there are no seasonal differences in length of activity bouts of wild and captive caribou; (4) there are no seasonal differences in length of daily time spent lying in captive caribou; (5) caribou cycles of activity are uniformly distributed over the 24-h period; (6) caribou exhibit synchronous activity within groups; and (7) caribou exhibit synchronous activity between groups. Evidence supporting a strategy of nychthemeral activity would include equal activity day and night. As daylength increased, we expected an increase in the number of cycles each day for a diurnal response, and a decrease in number of cycles each night for a nocturnal response. In nychthemeral animals, no seasonal changes in cycle number, cycle length, and daily time spent active and resting would be expected as a function of daylength *per se*. Nonetheless, because environmental components such as snow depth, hardness, and density, wind, cold temperatures, insect harassment, predation risk, and body condition vary between individuals, we expected to observe differences between wild and captive caribou (Fig. 1). These differences are due to constraints on the time, activity, or energy budgets of animals in the wild and, thereby, constitute an ecological cost associated with free existence. Therefore, we compared the number and length of cycles of activity and rest among months using data on captive caribou to further investigate the effects of seasonality when ecological costs are removed or minimized.

In terms of timing of activity to sunrise and sunset, we made 2 primary assumptions: if caribou were timing the beginning of daily activity to sunrise, all caribou should begin activity at or near sunrise; and individual caribou should show little or no variation in timing of the beginning of daily activity. Consequently, we predicted a high degree of synchrony between widely separated groups (at least in the beginning of the day).

Methods

Animals

Wild caribou: Data on activity were collected on free-ranging, adult (≥ 2 yr) female caribou of the Delta Caribou Herd (DCH) in interior Alaska using Wildlink radiocollars (Wildlink, Inc., ® St. Paul, MN, 55444). The DCH is located on the north side of the central Alaska Range (64°14' N, 148°34' W; 63°35' N, 146°14' W). We captured and instrumented 6 caribou females with radiocollars in late winter (26 March 1991), 10 in post-calving (1 June 1991), and 9 in the insect season (26 July 1991) by darting them from a helicopter. Darts contained a mixture of carfentanil (0.036 mg/kg body weight) and 100 mg xylazine. All captured animals were instrumented with Wildlink radiocollars that were equipped with VHF radiotransmitters and an activity counter. After collaring, caribou were given an intramuscular injection of penicillin (100 mg), a topical application of antibiotic powder, and the reversing agents naloxone (150 mg naloxone/mg carfentanil) and yohimbine (0.2 mg/kg body weight). Caribou were given ≥ 4 days to recover before collection of data began. Presumably, a 4-day period of recovery was adequate because collared caribou behaved analogously to uncollared caribou (determined from direct observations of activity budgets of collared and uncollared caribou located in the same group). Collared caribou remained spatially and visually separated from other collared caribou throughout the study periods (i.e., in separate groups, not visible to each other). Collars were retrieved at the completion of each sampling period.

Data on 24-h activity collected on female caribou of the DCH were recorded by a mercury tip-switch that registered a count (i.e., activity count) each time the collar was tilted. Systems for activity monitoring based on tip-switch technology cannot discriminate between specific activities (e.g., standing, feeding, walking) but we could accurately discriminate active from resting bouts (Chapter 3). Activity counts were recorded in 1-h intervals and summarized over 24-h periods for analysis.

Relationships between activity counts recorded by Wildlink collars and caribou behavior were evaluated using captive male and female caribou at the Large Animal Research Station (LARS), Institute of Arctic Biology, University of Alaska Fairbanks (Chapter 4). The "resting threshold" is a critical concept for the purposes of determining activity levels of radiocollared caribou. This threshold is defined as the sum of activity counts above which an animal is likely to have been active; this variable was determined for each season, at a variety of activity levels of caribou (Chapter 2). Specifically, the resting threshold is defined as 20% of the largest activity count per day. The threshold was established to partition each 24-h period into resting and active bouts. Thus, an active bout was defined as the sum of consecutive 1-h intervals during which activity counts exceeded the resting threshold. The number of active and resting bouts per day, the mean length of resting and active bouts per day, and the total time spent active and resting per day were calculated from data on activity counts.

Captive caribou: Activity patterns were determined monthly on captive caribou housed in 1-ha pastures at LARS. Captive caribou had free grazing on a brome-hay pasture, supplemented with ad libitum high quality feed pellets (Quality Texture, Alaska Mill and Feed Co., Anchorage, AK 99510). We collected data on activity from 6 adults (3 males, 3 females) using 24-h behavioral watches with focal-animal sampling (Altmann 1974). Behavioral categories included: lying with head down; lying with head up; standing; cratering; feeding; grazing; walking; running; sparring; playing; nursing; and attempted nursing. We used the resting threshold to categorize resting and active bouts, calculated the mean duration of these bouts, and then determined the daily time spent active, and daily time spent resting. Active and rest cycles and their lengths were determined simultaneously with Wildlink radiocollars.

Photosensitive halogen lights (500 watts) were used to illuminate the pasture at night when night-vision equipment was not available, so that observers could locate the caribou. When we wanted 24-h data without the use of lights, and when night-vision equipment was not available, we collected data using Wildlink radiocollars. Activity counts were summed in 1-h intervals and summarized over 24-h periods for analysis as was done for DCH. Comparisons were made between activity patterns of caribou under lighted conditions and activity patterns of caribou collected either using Wildlink collars or night-vision equipment on 3 occasions to determine if lights affected caribou activity. Specifically, we used t-tests (Zar 1984) to compare activity collected on nights when lights were used with activity collected without the use of lights. Variables we analyzed included the mean number of active and resting bouts, the mean duration of these bouts, and the daily time spent active and resting. Significance was assessed at $\alpha = 0.05$ for these tests and for all other tests reported herein.

Diurnal, nocturnal, crepuscular, or nychthemeral activity?

We tested the hypothesis of equal activity day and night (i.e., nychthemeral behavior) using 4, 24-h data sets on 3 captive adult caribou (1 male, 2 females) at LARS and 5 consecutive days of 24-h data collected on 6 adult female caribou of the Delta herd. Data sets were collected during periods of 12-h of day and 12-h of night in late winter (March 1993) and were conducted using Wildlink radiocollars and night-vision equipment for caribou at LARS. Data sets were collected in late winter (first week of April 1991) and were gathered with Wildlink radiocollars for caribou of the Delta herd. We used 3 independent activity variables, each affected by seasonal changes in the environment, as measures of caribou activity: (1) the mean number of cycles of activity and rest, day and night; (2) the mean duration of daytime and nighttime cycles of activity and rest; and (3) the daily time spent active and resting during day and nighttime hours. We made comparisons between day and night using t-tests (Zar 1984).

We tested the hypothesis of equal activity (nychthemeral) throughout the year and across physiological seasons using 24-h data sets collected each month over a period of 2 years on 6 adult captive caribou. The physiological seasons were originally delimited for the Porcupine Caribou Herd (Russell et al. 1993) and, thus, were modified to account for differences due to latitudinal location between caribou at LARS and caribou of the Porcupine herd (Table 1). We made comparisons of the number of cycles of activity and rest and the length of activity and resting bouts across physiological seasons using multiple analysis of variance (MANOVA) with a repeated measures design (Johnson and Wichern 1988) using PROC GLM procedures (SAS Institute Inc. 1985). When significant differences occurred, Tukey's Studentized Range (HSD) multiple comparison of mean effects was used to determine which effects were different (Johnson and Wichern 1988). Additionally, we compared daily time spent lying across seasons to

Table 1. Physiological seasons of caribou of the Porcupine Caribou Herd (Russell et al. 1993) and interior Alaska herds (i.e., LARS (1991-1993) and Delta caribou herds (1991); this study). These seasons represent times of the year that a caribou is in a particular energetic or nutritional state and vary according to the conditions of a particular year.

	Herd	
Season	Porcupine	Interior
Midwinter	11 January - 20 February	1 January - 1 March
Late winter	21 February - 31 March	2 - 31 March
Spring	1 - 30 April	1 - 30 April
Spring migration	1 - 19 May	1 - 10 May
Pre-calving	20 - 31 May	11 - 16 May
Calving	1 - 10 June	17 - 27 May
Post-calving	11 - 20 June	28 May - 10 June
Movement	21 - 30 June	11 - 18 June
Early summer	1 - 15 July	19 - 30 June
Mid summer	16 July - 8 August	1 - 31 July
Late summer	9 August - 7 September	1 - 30 August
Fall migration	8 September - 7 October	31 August - 20 September
Rut	8 - 31 October	21 September - 19 October
Late fall	1 - 30 November	20 October - 20 November
Early winter	1 December - 10 January	21 November - 31 December

determine if lying time varied in response to daylength using MANOVA. Again, Tukey's studentized range (HSD) multiple comparison of mean effects was used if a significant overall difference was noted.

We further tested the hypothesis of equal activity in the 3 physiological seasons (late winter, post-calving, and the insect season [referred to as midsummer by Russell et al. 1993]) for which we have activity data on wild, free-ranging caribou of the Delta herd. We made comparisons of the number of daily cycles of activity, the length of active and resting bouts, and the daily time spent active and resting using one-way ANOVA (Zar 1984).

Timing of activity to sunrise and sunset?

Wild caribou: We tested the hypothesis that caribou are as likely to be inactive as active at or near sunrise using activity data collected on the DCH. Alternatively, caribou may time activity to sunrise and be active primarily at sunrise and sunset (i.e., crepuscular). We approached the question in 3 ways: First, we summed the number of caribou active and inactive (based on the resting threshold) at hourly intervals before and after sunrise to determine if caribou were systematically active at sunrise, an hour before, or an hour after sunrise in late winter. These sums then were compared using the Wilcoxon two-sample test (Conover 1980). Second, we calculated the time interval between sunrise and the beginning of activity for each individual caribou for each day of the late-winter period. A two-way ANOVA was used to compare the variability of this time interval between animals and days (Zar 1984) with animal and day as class variables.

Captive caribou: We used circular statistics (Batschelet 1981) to test the hypothesis that activity cycles of caribou are uniformly, or randomly, distributed over 24-h, to determine whether caribou exhibited a peak of activity, and where the peak hour of activity occurred each day. We determined the time of the beginning of each activity cycle for caribou at LARS and then conducted circular statistics to determine if there was a peak time of activity for the entire day. The Raleigh test for randomness was used to test the specific null hypothesis that the activity pattern was uniformly distributed, that is, whether there was any statistical evidence of one-sidedness or directedness (Batschelet 1981). The mean vector length, *r*, was the test statistic such that if *r* was sufficiently large ($P > 0.05$), the hypothesis of randomness was rejected. The day was divided into 2 parts; midnight to noon and noon to midnight; and the analysis was conducted on one-half days (if caribou engage in crepuscular activity we expected the hypothesized peak of activity at sunrise to be masked by the hypothesized pre-sunset peak of activity [or vice versa] when analyzed statistically). In this instance, we tested the separate hypotheses that nighttime activity (midnight to noon) was uniformly or randomly distributed and that daytime activity (noon to midnight) was uniformly or randomly distributed, (ie., there was no significant peak of activity during the night or day). The test for uniformity of activity was repeated for caribou of the Delta herd but was confined to testing for a peak of activity at or near sunrise (midnight to noon) because of missing data that occurred at or near sunset each day.

Within- and between-group synchrony?

We investigated within-group synchrony of activity using the 24-h data sets collected on caribou at LARS. Caribou were considered to be within the same group as they were likely aware of, and often in sight of, all other caribou housed at LARS. Between-group synchrony was limited to comparisons made on wild caribou of the Delta herd as each individual caribou was in a distinct group and was spatially and visually separated from each of the other radiocollared caribou. Comparisons are graphical and qualitative in nature because of differences in techniques of data collection between captive and wild caribou.

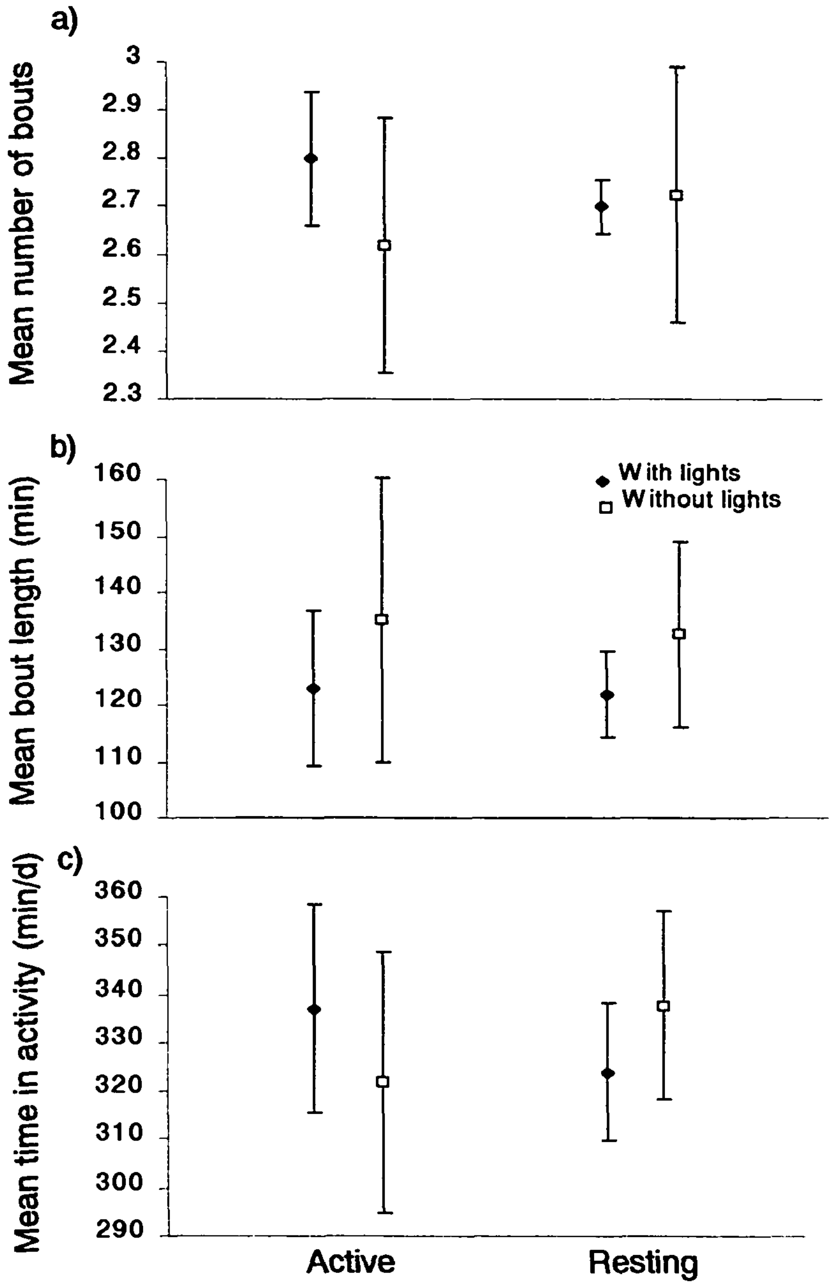

Fig. 2 Effects of artificial lighting on activity of caribou at the Large Animal Research Station, Alaska. Comparison of mean (± SE) a) bout number, b) bout lengths (min), and c) time in daily activity (active and resting, min/d) of 3 adult (≥ 2 years) caribou (1 5-yr-old male, 2 6-yr-old females) on nights with and without the use of photosensitive halogen lights. Data were collected in March 1993.

Results

The use of lights during behavioral observations at night did not affect the mean number or the mean length of activity bouts exhibited by captive caribou as compared with observations conducted without the use of lights (Fig. 2). Mean daily time spent resting and active also was unaffected by the use of lights. Mean number of active bouts on nights with lights were not significantly different from those without lights ($P = 0.24$ from a 2-sample t-test, df = 11). The mean number of active bouts of caribou at LARS was 2.8 ± 0.27 (Mean ± 95% C. I.) on nights with lights and 2.6 ± 0.49 on nights when data were collected without the use of lights. Caribou rested 2.7 ± 0.12 times on nights with lights and 2.7 ± 0.49 times when lights were not used. Mean number of resting bouts on nights with lights were not significantly different from those without ligths ($P = 0.47$; df = 11) (Fig. 2a). Lengths of active bouts were equivalent on nights with lights (123 ± 27 min) and nights without them (129 ± 41 min) ($P = 0.41$; df = 10) as were resting bout lengths (122 ± 15 min with lights and 127 ± 27 min without lights ($P = 0.38$; df = 9)) (Fig. 2b). Finally, the use of lights did not affect the mean time spent active on nights with lights (337 ± 42 min) and on nights without lights (322 ± 53 min) ($P = 0.34$; df = 11) or mean time spent resting on nights with lights (324 ± 28 min) and on nights without them (338 ± 38 min) ($P = 0.29$; df = 11) (Fig. 2c).

Daily activity patterns

The null hypothesis of equal activity day and night was supported for caribou at LARS and caribou of the Delta herd. Caribou at LARS exhibited equal activity day and night during late winter in observations collected on days of equal day and night, thus, supporting the hypothesis of equal activity. Specifically, caribou at LARS engaged in 2.7 ± 0.37 active bouts during the day and 2.8 ± 0.47 active bouts at night ($P = 0.86$; df = 16), whereas there were 2.6 ± 0.41 resting bouts were during the day and 2.6 ± 0.43 at night ($P = 0.80$; df = 16) (Fig. 3a). Lengths of active bouts did not differ significantly between day and night, 155 ± 57 min and 133 ± 67 min, respectively ($P = 0.15$; df = 16) (Fig. 3b). Caribou at LARS rested on average for 126 ± 55 min during daytime bouts

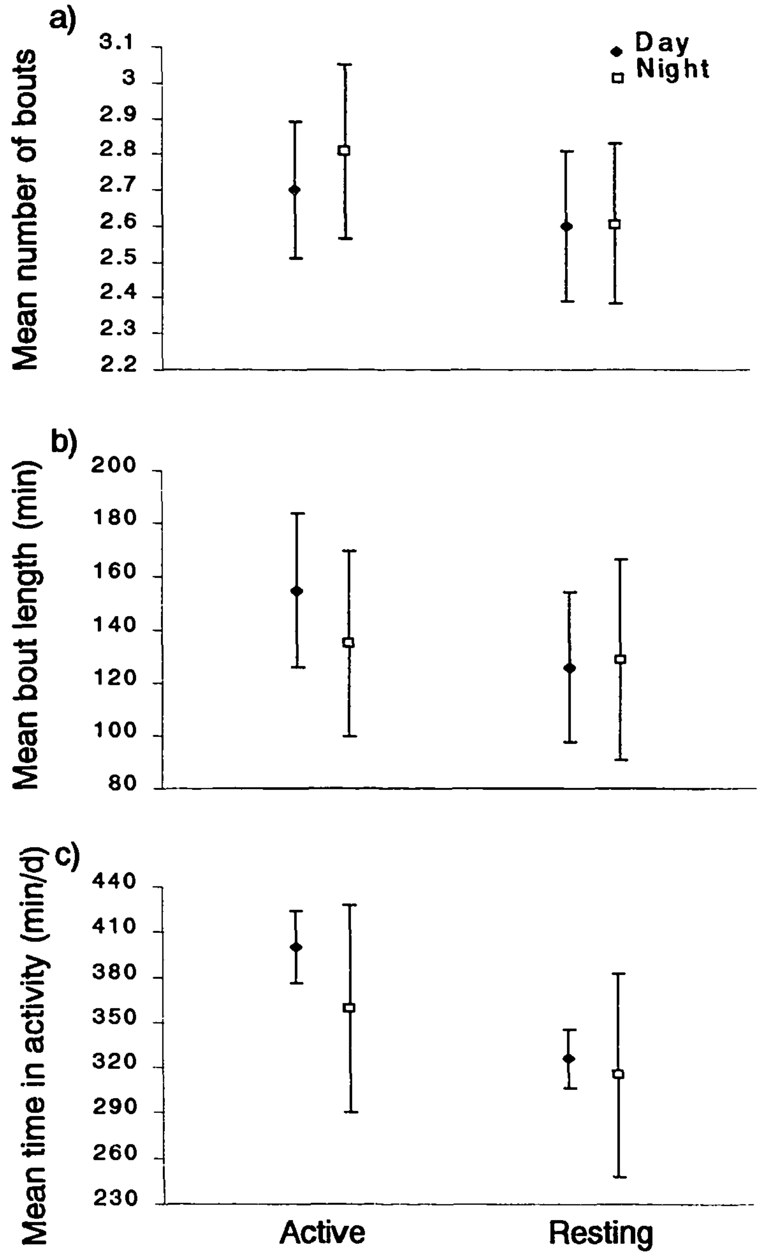

Fig. 3 Daytime and nighttime activity of caribou at the Large Animal Research Station, Alaska. Comparisons are of mean (± SE) a) bout number, b) bout lengths (min), and c) time in daily activity (active and resting, min/d) of 3 adult (≥ 2 years) caribou (1 5-yr-old male, 2 6-yr-old females) collected during daytime and nighttime hours. Date were collected in March and April 1993.

and 127 ± 73 min during nighttime bouts ($P = 0.93$; df = 16) (Fig. 3b). Finally, time spent active during daylight was equivalent (400 ± 47 min) to time spent active at night (354 ± 129 min) ($P = 0.08$; df = 16) as was daily time spent resting (326 ± 37 min), during daylight, and 312 ± 127 min, at night) ($P = 0.55$; df = 16) (Fig. 3c).

Caribou of the Delta herd exhibited equal activity day and night during late winter in observations collected on days of equal day and night, thus, supporting the hypothesis of equal activity. Specifically, caribou of the Delta herd engaged in 2.7 ± 0.12 active bouts during the day and 3.0 ± 0.14 active bouts at night ($P = 0.06$; df = 21), whereas there were 2.7 ± 0.12 resting bouts were during the day and 3.0 ± 0.25 at night ($P = 0.11$; df = 20) (Fig. 4a). Lengths of active bouts did not differ significantly between day and night, 155 ± 9 min and 135 ± 10 min, respectively ($P = 0.06$; df = 28) (Fig. 4b). Caribou of the Delta herd rested on average for 126 ± 12 min during daytime resting bouts and 115 ± 11 min during nighttime resting bouts ($P = 0.25$; df = 28) (Fig. 4b). Finally, time spent active during daylight was equivalent (430 ± 29 min) to time spent active at night (399 ± 29 min) ($P = 0.22$; df = 28) as was daily time spent resting (331 ± 27 min), during daylight, and 318 ± 20 min, at night) ($P = 0.35$; df = 26) (Fig. 4c).

We rejected the hypothesis of equal activity among seasons for captive caribou at LARS and wild caribou of the Delta herd. Specifically, the number of cycles exhibited by captive caribou differed significantly among seasons (F = 3.98; df = 8, 20; $P = 0.006$) (Fig. 5). Tukey's pairwise comparisons, however, did not elucidate any significant differences between means. Similarly, there was a significant difference in mean duration of active bouts among seasons (F = 5.28; df = 8, 21; $P = 0.001$) (Fig. 6a) with midsummer active bout lengths differing significantly from active bout lengths in autumn. Mean duration of resting bouts were equivalent among seasons (F = 1.67; df = 8,21; $P = 0.166$) (Fig. 6a) as was the daily time spent resting (F = 2.19; df = 8, 21; $P = 0.07$) (Fig. 7a). Daily time spent active is the reciprocal of daily time resting so it was not analyzed.

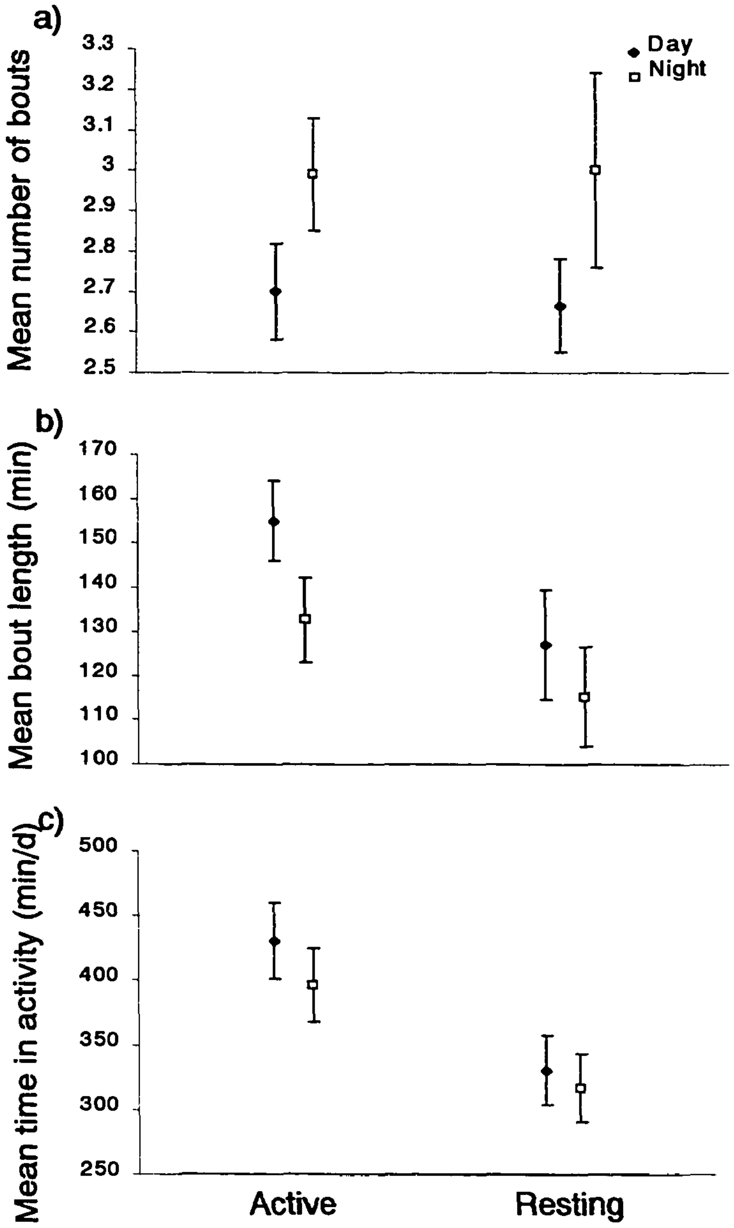

Fig. 4 Daytime and nighttime activity of caribou of the Delta Caribou Herd, in Alaska. Comparisons are of mean (± SE) a) bout number, b) bout lengths (min), and c) time in daily activity (active and resting, min/d) of 6 adult (≥ 2 years) female caribou collecting during daytime and nighttime hours. Data were collected in April 1991.

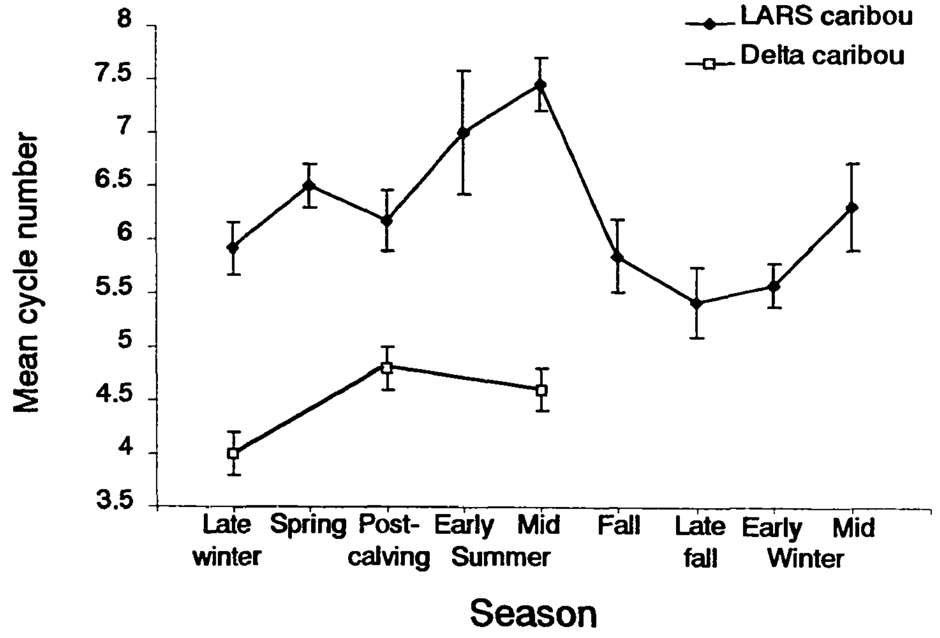

Fig. 5 Seasonal trends in activity cycles of caribou at the Large Animal Research Station (LARS) and in the Delta herd, in Alaska. Mean (± SE) cycle number of 3 adult (≥ 2 years) caribou (1 5-yr-old male, 2 6-yr-old females) at LARS (data collected January 1991 through July 1993) and adult female caribou of the Delta caribou herd (n = 6 in late winter, 10 in post-calving, and 9 in the insect season). Data on caribou of the Delta herd were collected in 1991.

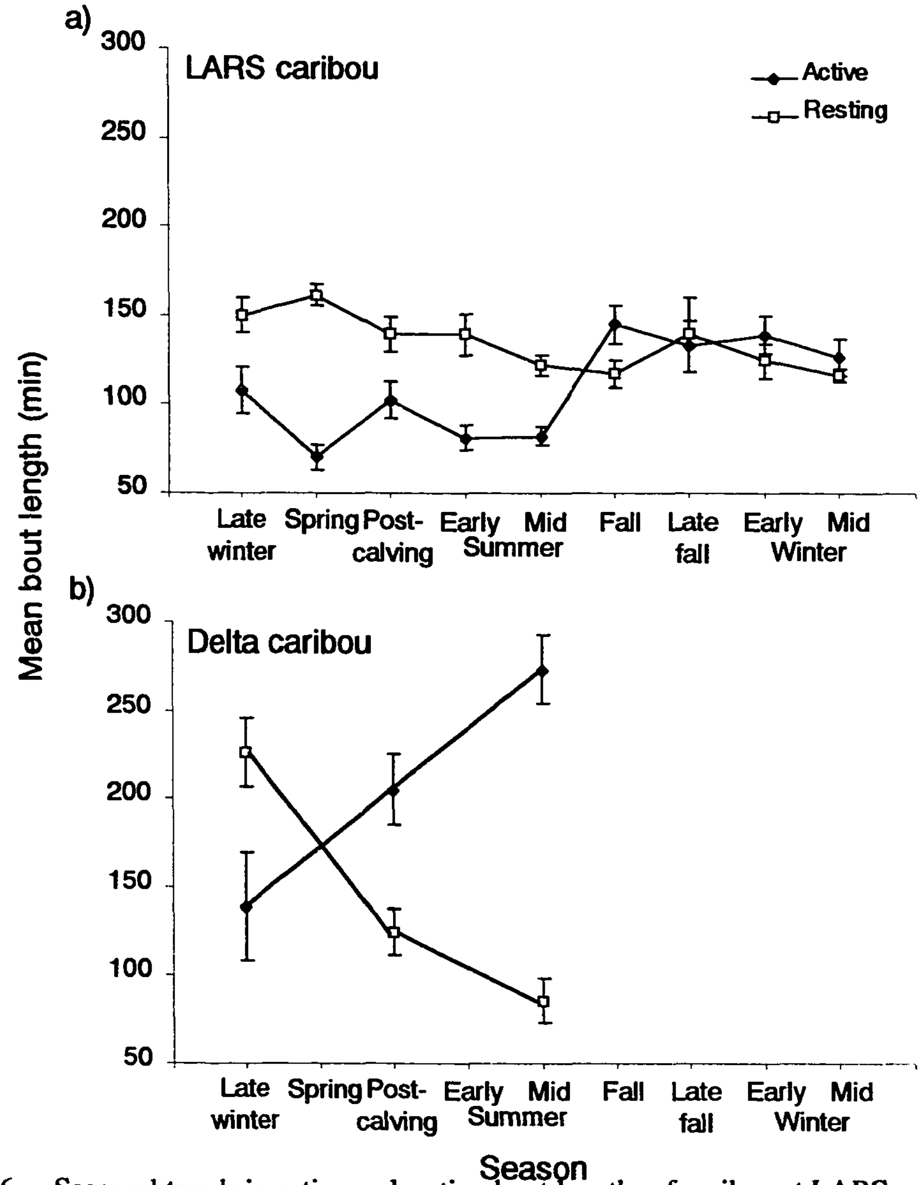

Fig. 6 Seasonal trends in active and resting bout lengths of caribou at LARS and caribou of the Delta herd, in Alaska. Mean (± SE) active and resting bout length (min) of a) 3 adult (≥ 2 years) caribou (one 5-yr-old male, two 6-yr-old females) at LARS (data collected January 1991 through July 1993) and b) adult female caribou of the Delta caribou herd (n = 6 in late winter, 10 in post-calving, and 9 in the insect season). Data on caribou of the Delta herd were collected in 1991.

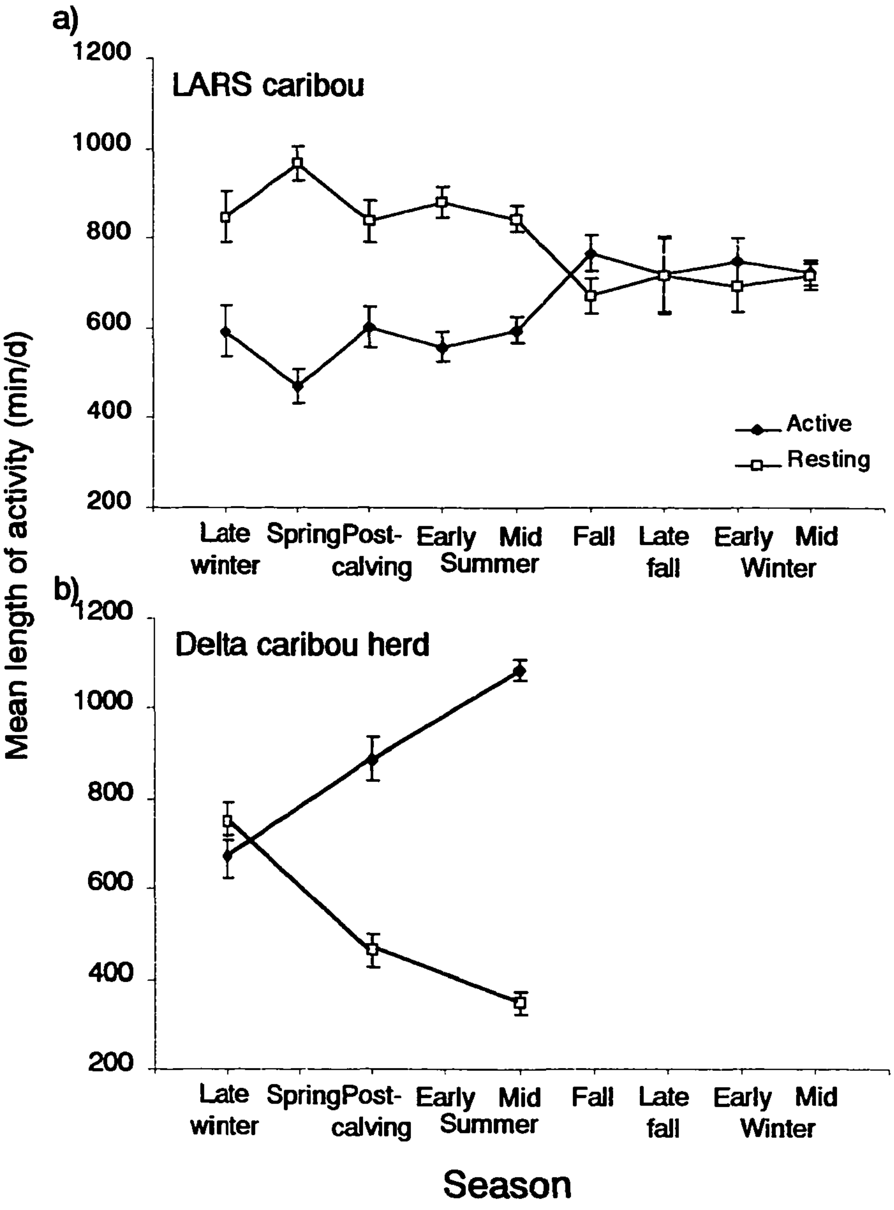

Fig. 7 Seasonal trends in daily activity of caribou at LARS and in the Delta herd, in Alaska. Mean (± SE) length of daily activity (active and resting; min/d) of a) 3 adult (≥ 2 years) caribou (one 5-yr-old male, two 6-yr-old females) at LARS (data collected January 1991 through July 1993) and b) adult female caribou of the Delta caribou herd (n = 6 in late winter, 10 in post-calving, and 9 in the insect season). Data on caribou of the Delta herd were collected in 1991.

Caribou of the Delta herd engaged in significantly fewer cycles in late winter (3.8 ± 0.69) than in post-calving (4.8 ± 0.45) or midsummer (4.6 ± 0.43) (F = 2.99; df = 2, 89; $P = 0.055$) (Fig. 5). Length of active bouts differed significantly among the 3 seasons (F = 7.68; df = 2, 89; $P = 0.0008$) with active-bout lengths being longest during insect harassment (273 ± 37 min), intermediate in post-calving (205 ± 39 min) and shortest in late winter (139 ± 59 min) (Fig. 6b). Lengths of resting bouts also were significantly different among the 3 seasons (F = 18.25; df = 2, 89; $P = 0.0001$). Resting bouts in late winter were longest (226 ± 38 min) followed by post-calving (125 ± 26 min) and midsummer (86 ± 24 min) (Fig. 6b). Finally, the daily time spent resting differed significantly among seasons (F = 23.42; df = 2,89; $P = 0.0001$) with the longest daily resting occurring in late winter (750 ± 98 min) followed by post-calving (460 ± 65 min) and midsummer (345 ± 62 min) (Fig. 7b).

Timing of activity

The null hypothesis of uniformly distributed activity was supported. Caribou of the Delta herd generally did not time activity to sunrise and LARS caribou did not time activity either to sunrise or sunset, thus, supporting the hypothesis of uniformly distributed activity. Caribou of the Delta herd were as likely to be inactive as they were to be active 0.5 h before sunrise ($P = 0.47$; df = 8) and this trend continued generally throughout the day (Fig. 8a). At sunrise, however, caribou were more likely to be inactive than active ($P = 0.05$; df = 8). Comparatively, caribou of the Porcupine herd, located in the same group, began activity at sunrise (Russell et al. 1993) and maintained a high degree of inter-individual synchrony of activity throughout the day (Fig. 8b). There were no differences in the mean time interval between beginning of daily activity and sunrise among animals (F = 1.89; df = 5, 24; $P = 0.13$) or days (F = 0.18; df = 4, 25; $P = 0.95$), likely because of the high degree of variability of timing of activity within individual caribou ($r^2 = 0.28$ for animals and $r^2 = 0.03$ for days) and small sample sizes (6 animals, 5 days) (Fig. 9).

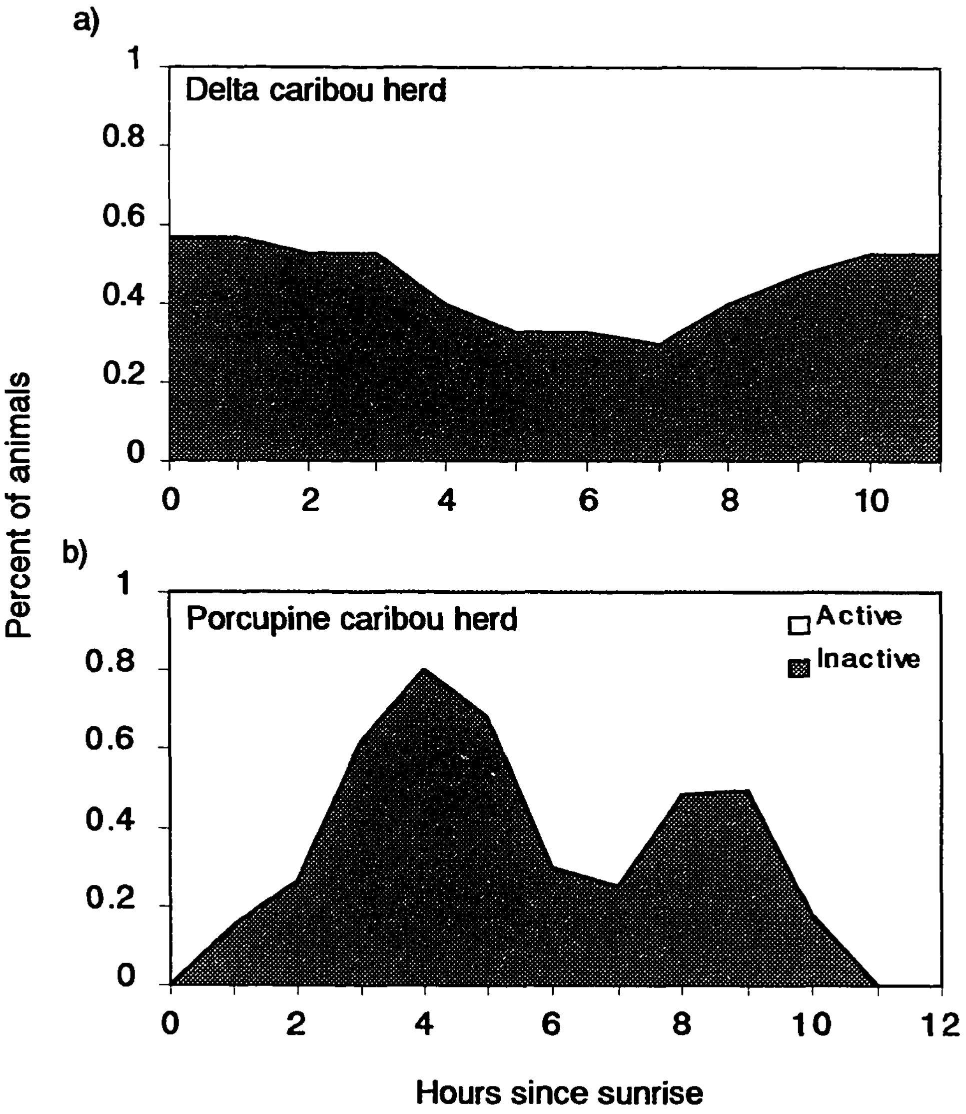

Fig. 8 Activity in relation to sunrise for caribou of the Delta and Porcupine herds, in Alaska. Data shown are percent of animals lying as a function of time since sunrise. Hourly Wildlink activity counts were used for caribou of the Delta herd (late winter, 1991) a) and 15 min scans in late winter for caribou of the Porcupine caribou herd b). Data are for winters of 1979-80 and 1981-82, Russell et al. (1993).

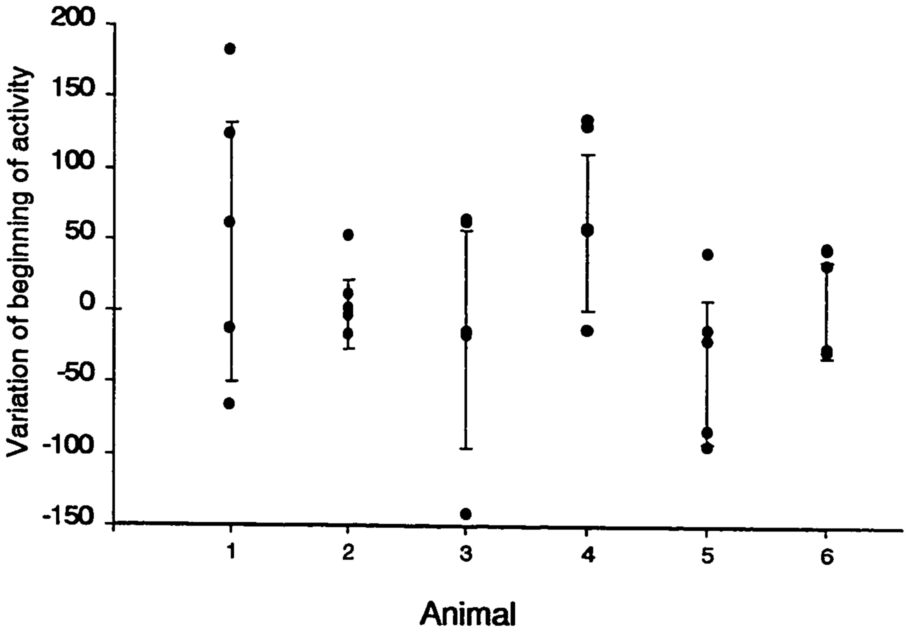

Fig. 9 Variation of the beginning time of daily activity in relation to sunrise in 6 adult (≥ 2-yr-old) female caribou of the Delta caribou herd in late winter (1 - 5 April 1991), in Alaska. Bar represents ± 1 SD.

Caribou at LARS exhibited uniform (i.e., random) activity year-round, as deduced using circular statistics. Mean vector lengths, r, for 24-h days, ranged from 0.36 to 0.025, with associated P values of 0.11 and 1.00, and generally were at or near r = 0.17 (P = 0.71). Mean vector lengths remained insignificant even after dividing the 24-h day into 12-h days (r = 0.15; P = 0.82) and 12-h nights (r = 0.16, P = 0.74). Caribou of the Delta herd exhibited correspondingly uniform nighttime patterns of activity (midnight to noon) with mean vector lengths ranging from 0.33 to 0.08 (P = 0.30 and 0.92, respectively).

Within- and between-group synchrony

The hypothesis of synchronous activity within a group of caribou was supported. Caribou at LARS exhibited a high degree of within-group synchrony in all seasons (Fig. 10), as did those instrumented caribou of the DCH that opportunistically were located within the same group on 8 June 1991 (Fig. 11). The hypothesis of synchronous activity between groups of caribou, however, was rejected. Caribou of the Delta herd that were not located in the same group (all caribou during late winter and the insect season and most caribou during post-calving) did not exhibit synchrony (Fig. 8a).

Discussion

Captive caribou exhibited nychthemeral activity patterns, as evidenced by the occurrence of equal activity day and night when darkness was present in winter (Fig. 3). This contrasts with the primarily diurnal patterns reported for reindeer on the Seward Peninsula (Collins and Smith 1989). Reindeer in the Collins and Smith study were subjected to ecological pressures not experienced by the captive caribou. Predator avoidance is an important factor controlling *Rangifer* activity and, hence, the prevalence of diurnal activity of reindeer inhabiting the Seward Peninsula in winter could be because of increased sightability of predators in this open terrain. Predation may not be the only explanation, however, as caribou of the Delta herd were foraging in open terrain and on ridge tops were no more active in daytime than nighttime (Fig. 4). We suggest that the

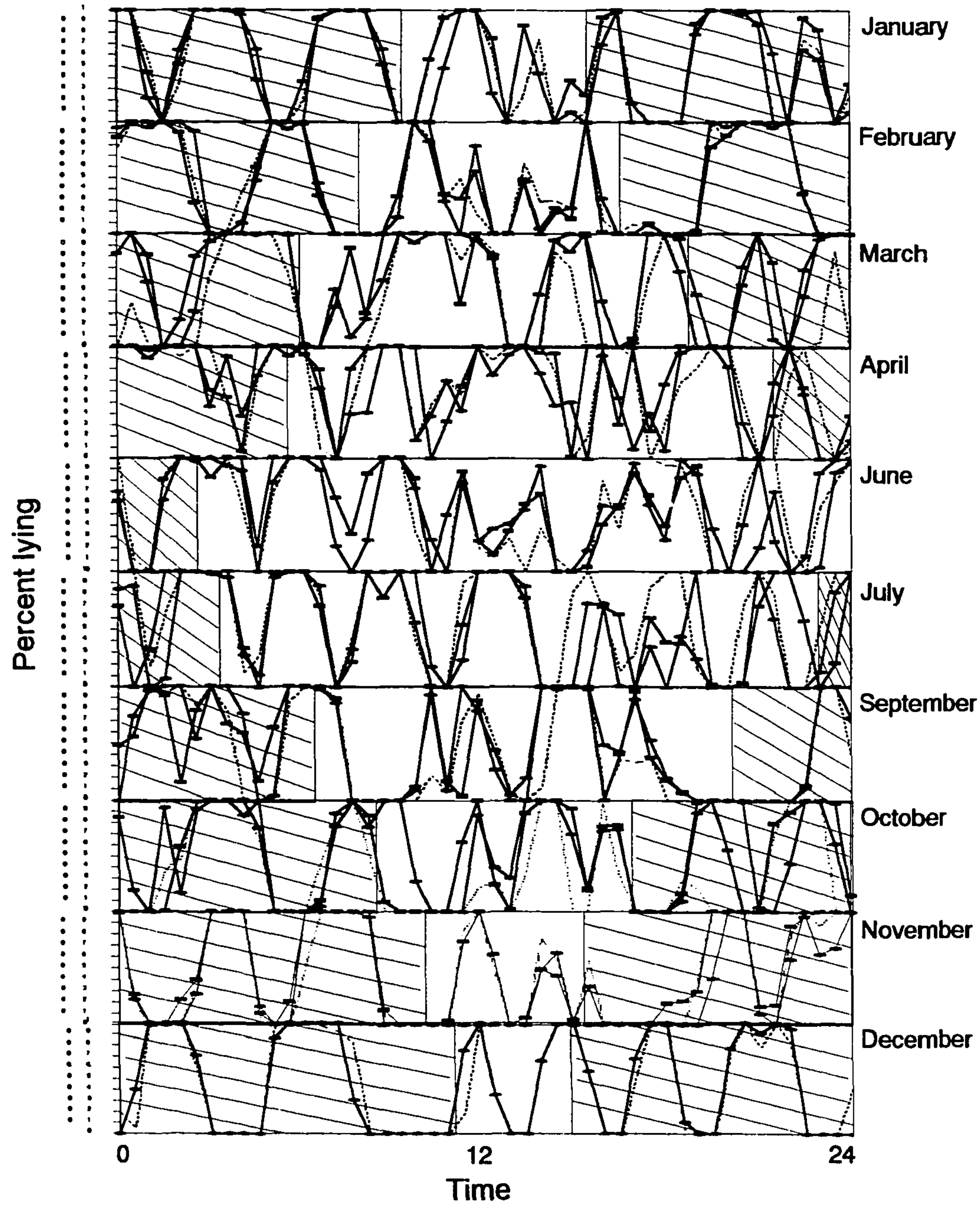

Fig. 10 Seasonal activity patterns of adult (≥ 2 years) caribou (1 5-yr-old male, 2 6-yr-old females) at LARS (data collected January 1991 through July 1993), in Alaska. Activity patterns are % lying through time.

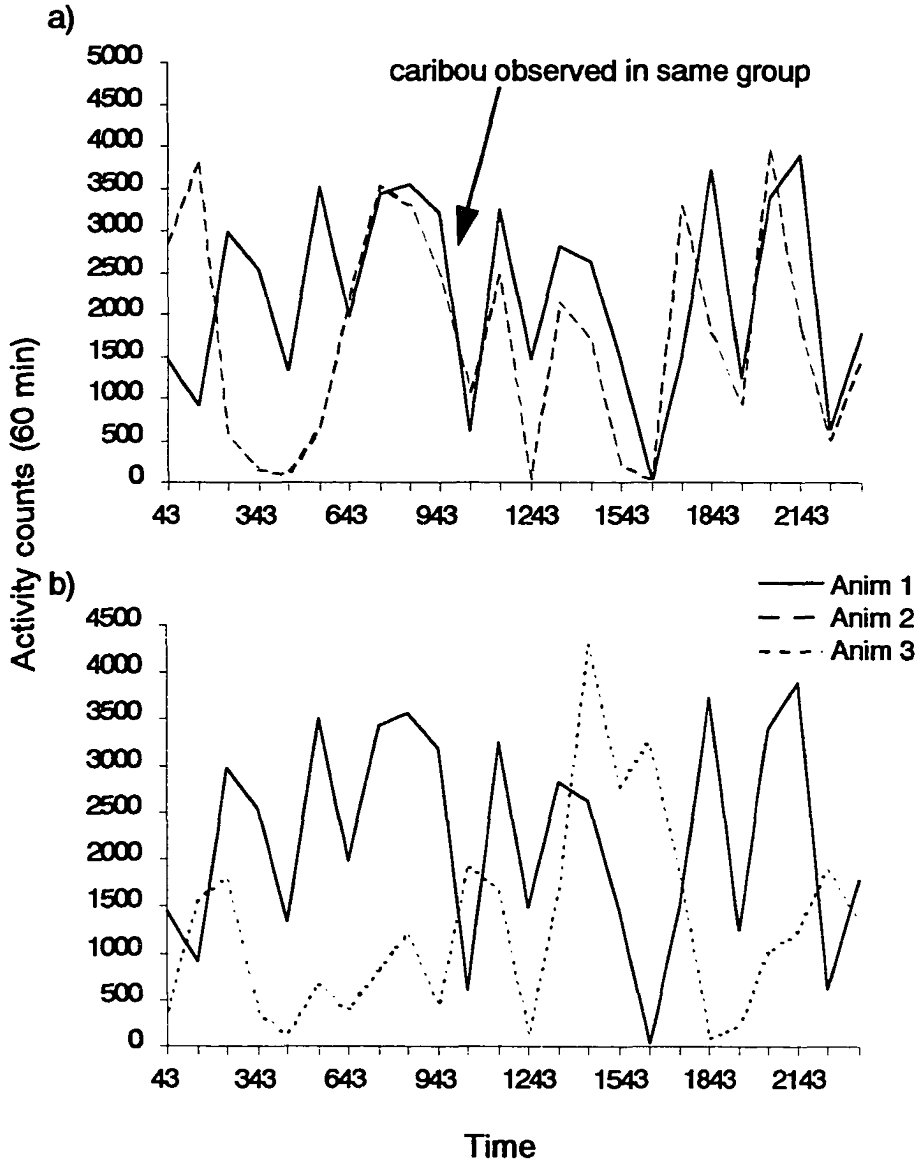

Fig. 11 Examples of a) synchronous and b) asynchronous activity of caribou as deduced from activity-monitoring radiocollars. Activity counts (60 min) of 3 adult (≥ 2-yr-old) female caribou of the Delta caribou herd on 12 June 1991, a) in the same group and b) in separate groups, over a 24-h period, in Alaska.

nychthemeral activity exhibited by caribou when most ecologically modifying factors are minimized reflects a basic and, perhaps, innate rhythm that maximizes digestive function. Deviation from nychthemeral activity would then reflect modification in reaction to ecologically important influences. Caribou of the Delta herd were subjected to record-deep snow in the year of this study and were in the poorest body condition ever recorded for this herd (Chapter 2). We suggest the need for regular feeding bouts (on these limited, low quality resources) was possibly the overriding factor driving activity and hence a nychthemeral pattern of activity was documented.

When time and ecologically costly responses are minimized, caribou should exhibit behavior reflecting nutritional conditions, seasonal reproduction, and evolved adaptive traits. For the captive caribou at LARS, level of nutrition was high and other ecological costs were minimal, except for mild insect harassment in June and early July. Mean duration of resting bouts and the daily time spent resting were equivalent among seasons (Figs. 6a and 7a) as was the mean number of cycles (Fig. 5). A statistically insignificant increase in length of active bouts (and daily time spent active) occurred in post-calving caribou (Fig. 6a) and coincided with mosquito harassment in June. In autumn, lengths of active bouts increased significantly coincident with rutting activity and were followed by a slow decline throughout winter (Fig. 6a). Although seasonal patterns of daily time spent resting (and active) mirror those of mean duration of active bouts, these changes were marginally not significant ($P = 0.07$) (Fig. 7a). These results show that major events such as calving and lactation influence daily activity and resting cycles minimally. Rutting behavior, however, increases duration of active bouts. Seasonal shifts in activity patterns attributable to calving, lactation, and rutting activity should be expected in wild caribou populations.

In contrast to captive caribou, those of the Delta herd exhibited distinct differences in activity cycles among the 3 seasons. Late winter caribou exhibited few cycles of activity (Fig. 5) with short active and long resting bouts (Fig. 6b). In late winter, caribou spent significantly more time resting each day than post-calving or insect-harassed (midsummer) caribou (Fig. 7b). Similar trends were noted in activity patterns of moose (Risenhoover 1986, Van Ballenberghe and Miquelle 1990) with fewer bouts, longer bouts of resting, longer daily time spent resting, and shorter daily time spent active in winter than in summer. Moose exhibited a peak in the length of active bouts and daily time active in early summer, associated with peak phenology of shrubs (Van Ballenberghe and Miquelle 1990). In midsummer, caribou responded to insect harassment by engaging in short resting bouts, long bouts of activity (Fig. 6b), and less resting time (Fig. 7b) than did post-calving caribou. If activity were changing relative to daylength (i.e., increased activity with increased daylength), we would expect to see the greatest amount of activity in post-calving caribou (20.1 h of daylight) rather than in midsummer (17.4 h of daylight); the reverse was found, however. Number of daily cycles was not affected by environmental influences in post-calving or midsummer caribou (Fig. 5). The daily time spent resting for caribou in the insect season (350 min, 24% of day) is equivalent to lying times reported for caribou and reindeer under mild insect harassment at Prudhoe Bay and Hardangervidda (White et al. 1975). A further decrease in time spent lying to < 10% of the day would be expected for animals subjected to severe insect harassment.

Neither wild nor captive caribou timed activity to sunrise or sunset in this study. This result was unexpected as numerous authors have reported timing of activity to sunrise and sunset in *Rangifer* (Roby 1978, Collins and Smith 1989, Russell et al. 1993). Timing of activity to light is postulated to be adaptive in terms of predator avoidance and increased foraging efficiency through within-group cohesion (Estes 1974, Berry et al. 1985). Caribou at LARS, free from predation and other ecological costs, have no reason to time activity to sunrise and sunset, and they exhibited uniform (random) activity. Caribou of the Delta herd also exhibited random patterns of activity throughout the 24-h with no peak of activity at sunrise. A rigid definition of timing of activity to sunrise and sunset is lacking in the wildlife literature but is clear in the literature pertaining to circadian rhythms. When activity is timed to photoperiod, then an active period should begin predictably at a certain light (lux) threshold (Aschoff 1960). The variability for an individual between successive days should be small. Collins and Smith (1989) reported that the onset of morning activity of reindeer coincided with the beginning of morning twilight. Nonetheless, their data show that reindeer began activity 1 h before morning twilight on 13 February and at morning twilight on 7 March. Indeed, the activity period of these reindeer began at 0800 h on each day of the study (13 Feb, 22 Feb, 7 March), independent of sunrise. Likewise, wild caribou in our study exhibited considerable variability in the timing of daily activity with one individual beginning activity 1 h before sunrise on one day and 3 h after sunrise 3 days later (Fig. 9). For strictly diurnal species, initiation of activity is less variable. Dall's sheep (Ovis dalli), for example, began activity predictably at or near morning twilight, during each of 5 different months (Hansen 1996).

Timing of activity to sunrise should be an important component in maintaining between-group synchrony. If caribou time activity to sunrise, or some fixed intensity of light, then the incidence of between-individual and between-group synchrony should be high, at least at the beginning of the day. We tested this hypothesis using focal caribou that were located in widely separated groups in the Delta Herd. These caribou exhibited no between-individual and, therefore, no between-group synchrony (Fig. 8a). Within-group synchrony has been widely documented in *Rangifer* (Segal 1962, Thomson 1973, Curatolo 1975, Roby 1978, Boertje 1981, Collins and Smith 1989, Russell et al. 1993) and is evident in caribou at LARS (Fig. 10) and in the Delta herd (Fig. 11a). Additionally, Collins and Smith (1989) report that *Rangifer* successfully maintained within-group cohesion at night. Other studies of caribou do not report on between-group synchrony. Within-group synchrony is likely an adaptation to living in open-country and yields enhanced foraging efficiency and predator avoidance through group vigilance (Estes 1974). This behavior is not necessarily a photoperiodic-driven behavior.

Conclusions

Whereas many ungulate species exhibit diurnal and crepuscular activity, caribou appear inherently nychthemeral. This strategy of nychthemeral activity ensures regular feeding and rumination, which enhances foraging efficiency. This strategy is modified by environmental events (predation, food availability, weather) and can result in cycles that suggest a primarily diurnal activity for wild populations. Moreover, we suggest that monitoring of caribou 24-h activity patterns can be used to deduce environmental influence.

Our data do not support timing of daily activity to some analogue of light threshold, such as sunrise. Rather the initiation of activity probably resulted from the need to feed following a rumination bout. Because we documented highly synchronous group foraging, even in darkness, for captive caribou data suggest animals of different body size and productivity have similar cycles of rumination and feeding, or that some aspect of social facilitation coordinates these events. Caribou did not time activity to sunrise or sunset, hence, no cue was apparent that synchronized activity between groups.

CHAPTER 2: EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON ACTIVITY OF CARIBOU[2]

Abstract: Activity patterns of ungulates are affected by biotic (e.g., resource quality, resource availability, predation, and physiological condition) and abiotic factors (e.g., daylength, temperature, and wind). Theory suggests that consumption of forage of high nutritional quality results in short resting bouts and consumption of forage of low-quality results in long resting bouts. Additionally, highly available, high-quality forage was expected to correlate with short active bouts and less available, low-quality forage to correlate with long bouts. We tested these hypotheses for 4 caribou (Rangifer tarandus granti) herds in Alaska; the Denali Herd (63° N), the Delta Herd (64° N), captive caribou in Fairbanks (64° N), and the Porcupine Herd (69° N, winter; 72° N, summer). Caribou responded to forage quality and availability largely in a predictable manner in all seasons we evaluated (late winter, post-calving, and insect season). Specifically, caribou decreased lengths of active bouts and increased lengths of resting bouts in response to deep snow. In contrast, insect harassment resulted in longer active bouts and, correspondingly, shorter resting bouts by caribou. Results support suggestions that caribou of the Delta caribou herd were effected by low quality and availability of food in winter and low availability of food in summer.

Key words: activity cycles, forage quality, forage availability, insect harassment, Rangifer tarandus, weather.

Introduction

Daily activity patterns reflect behavioral choices as animals integrate allocation of resources to their reproduction, maintenance, and growth (Reimers 1980; Horn and Rubenstein 1984; Forchhammer and Boomsma 1995). For ruminants, digestive

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[2] Maier, J. A. K. and R. G. White. In Prep. Effects of biotic and abiotic factors on activity of caribou. Oikos 00:000-000.

adaptation results in an array of activity budgets as time is allocated to gathering food (an active component) and then ruminating and digesting it (a resting component) over a wide range of forage availability and quality. Paradigms, including energy maximization, grazing (intake) optimization, and time minimization (Forchhammer and Boomsma 1995), have resulted from research regarding foraging efficiency and activity budgets of ruminants. Such paradigms suggest that the active component of the daily activity budget consists of associated feeding behaviors such as searching for food, social interactions, predator avoidance, and seasonal productivity (e.g., rutting, calving, nursing, etc.). In its simplest form, the daily cycle of activity is composed of active and resting periods. The amount of time allocated to feeding in each active period largely reflects time taken to refill the rumen, which in turn relates directly to availability and distribution of resources (Allden and Whittaker 1970, Trudell and White 1981, Lundberg and Palo 1993). Time is devoted to rumination between each active period of feeding. Length of the rumination bout depends on mastication and digestion processes (Blaxter 1962, Hungate 1975), which are a function of both the quality and amount of food eaten during the preceding period of activity. Adaptive variation in both rumen-reticulum size and fill, therefore, would affect time devoted to rumination (Staaland et al. 1979). Thus, although forage availability is the strongest controlling factor over the active period and forage quality over the resting period, there clearly is an interaction between quality and availability that influences both the active and resting components (Fig. 12, Illius and Gordon 1992, Lundberg and Palo 1993, Forchhammer 1995). For example, scarcity of a particular type of forage, in theory, could result in a longer rumination period to ensure maximum digestion of nutrients (Lundberg and Palo 1993, Forchhammer 1995).

Based on our model of interactions between forage quality and availability (Fig. 12), the duration of both active and resting periods will increase as food availability and quality decline. Likewise, we predict that a decline in food availability leads to an increase in daily time spent grazing (Fig. 12d). This phenomenon is well documented in the field for deer (Odocoileus) (Allden 1962, Allden and Whittaker 1970, Young and Corbett 1972, Spalinger et al. 1988), but is refuted by general seasonal trends in which feeding time is maximized at peak biomass (Jingfors 1980, Oleson 1987). Long

a. Activity period

		Availability	
		High	Low
Quality	High	Shortest	Short
	Low	Short	Longest

b. Resting period

		Availability	
		High	Low
Quality	High	Short	Shortest
	Low	Longest	Long

c. # Cycles/day

		Availability	
		High	Low
Quality	High	Many	Most
	Low	Few	Fewest

d. Grazing time/day

		Availability	
		High	Low
Quality	High	Short	Short
	Low	Long	Longest

Fig. 12 Theoretical effect of resources, forage availability and quality, over the active and rest cycles of ruminants.

foraging bouts followed by long resting and rumination bouts are diagnostic of low quality of resources (Manteca and Smith 1994), which is a function of either low availability of forage, low quality of forage, or both (Fig. 12a, 12b). We hypothesize, however, that short foraging and resting-rumination bouts are diagnostic of high quality of resources, independent of resource availability, although animals would still modify length of foraging bouts to compensate for low abundance of food (Fig. 12a, b).

Temperate systems are characterized by seasonal patterns of forage quality and availability. Thus, seasonal changes in patterns of activity documented in caribou (Rangifer tarandus) have been attributed to changes in range quality and availability, as well as to extrinsic ecological events, such as weather (e.g., snowcover, wind) and insect harassment (White et al. 1975; Skogland 1984, 1989; Russell and Martell 1986; Russell et al. 1993). Circannual rhythms also may affect seasonal changes in activity patterns during rut and through changes in body condition within individuals (Roby and Thing 1985, Adamczewski et al. 1993).

Few studies adequately differentiate between forage quality and availability and some utilize a concept of availability of digestible nutrients (White et al. 1975, White and Trudell 1980, Forchhammer 1995). Russell and Martell (1986), however, discussed the relation between forage quality and availability and the length of resting bouts in caribou and suggest that mean duration of resting bouts is a good measure of habitat quality. Comparing bout lengths among groups, however, may be invalid if caribou time their activity to sunrise (Roby 1978, Russell and Martell 1986, Russell et al. 1993) because the mean length of the lying period is thought to be constrained by daylength during winter (Russell et al. 1993). Data in Chapter 1 show that caribou do not time activity to sunrise and, therefore, mean duration of resting-bout lengths could be used to compare across groups and within a season, provided that weather variables are consistent among groups (e.g., wind in winter; Skogland 1984).

Ecological events and heavy grazing because of density-dependent effects both can affect food quality and availability on seasonal ranges (McCullough 1979; Skogland 1984, 1989; Forchhammer and Boomsma 1995). Effects are not always independent, and interactions between ecological events and density-dependent overgrazing are expected as populations reach carrying capacity, where small ecological effects may have large effects on individuals and populations (Fowler 1981, Skogland 1985). Presumably, estimates of carrying capacity can be made if population size, range quality, and weather variables are measured (McCullough 1979). Range quality declines as a population approaches carrying capacity, a response to intense grazing pressure (McCullough 1979), a phenomenon that has been well documented in populations of Rangifer (Couturier et al. 1990, Skogland 1990). Indeed, the only time that carrying capacity truly can be estimated is when forage quality and availability are low and populations are, thus, nutritionally stressed. Populations at carrying capacity exhibit poor individual body condition, low twinning rates (in moose, Alces alces), postponed age of first reproduction, diminished recruitment rates, and abandonment of preferred and seasonally definitive ranges. Hypothetically, variation in food quality and availability would be expected to affect the active and rest cycles (Fig. 12). This hypothesis can be tested by comparing activity patterns of animals known through independent assessment to be using ranges with different forage quality or availability (Forchhammer 1995).

To test predictions associated with changes in forage quality and availability (Fig. 12), we compared the mean duration of resting and active bouts in several populations of caribou. Captive caribou at the Large Animal Research Station (LARS) in Fairbanks, which were given ad libitum good-quality forage, were compared with animals in the Delta Caribou Herd, which appears to have exceeded carrying capacity of its range (Fleischman 1990, Valkenburg 1994). In addition, we compared these data with literature values for the Denali (Boertje 1981, 1985) and Porcupine (Russell et al. 1993) herds, which were considered to be on very good and moderate-quality summer ranges, respectively. Because seasonal changes in activity are expected, between herd comparisons were made within each season. To reject the hypothesis that food availability and quality influence activity patterns we would need to find no differences between populations in their seasonal activity and lengths of resting bouts.

Methods

Captive caribou at the Large Animal Research Station (LARS; 80% adult (> 2 yr.) female) were stocked at 35 animals on a 3 ha range located in the Tanana Hills north of Fairbanks, Alaska (64°45' N, 147°45' W). The Delta Herd was declining, at the time of this study, and composed 6,000 caribou, located north of the central Alaska Range (64°14' N, 148°34' W; 63°35' N, 146°14' W). The 1,500 caribou of the Denali Herd, mostly located in Denali National Park, Alaska, centered at 63°30' N, 150°30' W, was at all time low numbers. The Porcupine caribou herd numbered 180,000 individuals ranging in a vast area of northeastern Alaska and northwestern Canada (65°0' N, 133°30' W; 70°0' N, 148° 0' W) and was at near maximum size for a number of years.

Forage quality and availability

Forage quality and availability was directly measured at LARS (UAF), estimated for the range of the Delta Caribou Herd (Valkenburg 1994), and reported from the literature for the Denali (Boertje 1981) and Porcupine (Russell et al. 1993) caribou herds. The diet of LARS caribou consisted of a brome-hay pasture, on which the caribou had free grazing, supplemented with ad libitum availability of high-quality feed pellets (Quality Texture, Alaska Mill and Feed Co., Anchorage, AK 99510) year-round. Nutrient analyses, including the Van Soest and proximate analyses, were conducted seasonally on the brome-hay pasture and pelleted rations (W. E. Hauer, pers. comm.). Forage quality and availability of the Delta Herd was inferred from long-term data on body-weights reported by Valkenburg (1993; Fig. 13) and from analysis of fecal pellets (Valkenburg 1994). Forage quality and availability for the Denali herd was documented by Boertje (1981) and for the Porcupine herd by Russell et al. (1993) for late winter and post-calving periods.

Environmental factors

Snow cover was measured for caribou at LARS and estimated for Delta caribou from Healy and Big Delta weather stations. Snow cover for the Denali herd was documented by Boertje (1981) and for the Porcupine herd by Russell et al. (1993).

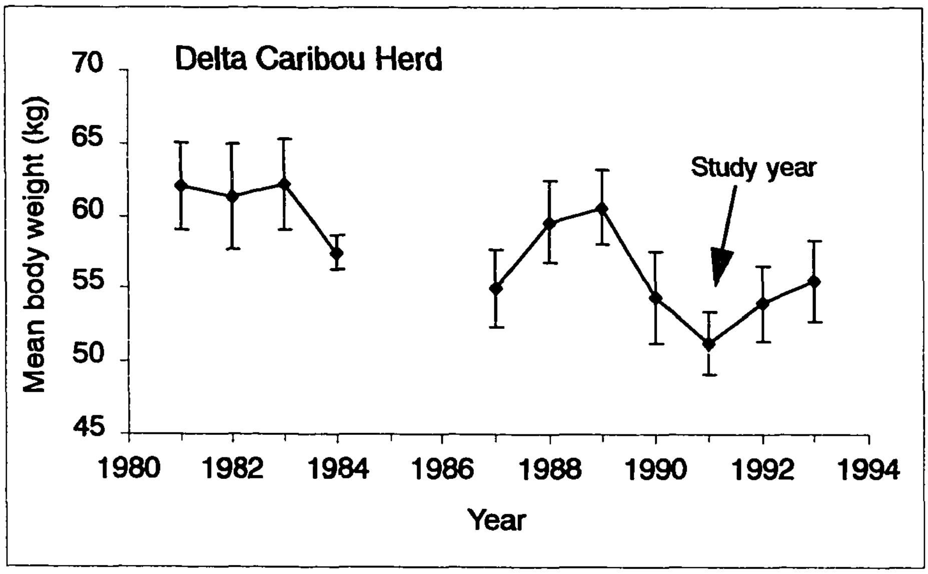

Fig. 13 Mean (± SE) body weights (kg) of 11-month-old female caribou of the Delta Caribou Herd in Alaska. Data were collected in April, from 1981-1984 and 1987-1993 (Valkenburg 1993). The year of the study was 1991.

Intensity of insect harassment endured by caribou at LARS and in the Delta Herd was estimated from visual observations of annoyance responses of caribou (White et al. 1975, Nixon 1991).

Resting and Active Bouts

Denali and Porcupine Caribou: The mean duration of active and resting bouts was obtained from the literature for the Denali (Boertje 1981, 1985) and Porcupine (Russell et al. 1993) Herds during late winter and the post-calving period.

Delta Caribou: Data on wild caribou of the Delta Herd were collected in each of 3 seasons: late winter, post-calving, and the insect season. We collected data on 24-hour activity cycles for Delta Herd females using Wildlink radiocollars (Wildlink, Inc., ® St. Paul, MN, 55444). Activity was recorded by a mercury tip-switch that registered a count (i.e., activity count) each time the collar was tilted (Kitchens et al. 1993, Murphy et al. 1994). Systems for monitoring of activity based on tip-switch technology cannot discriminate between specific activities (e.g., standing, feeding, walking) but can accurately depict active and resting bouts. Activity counts were recorded in 0.5-h (late-winter) or 1-h (post-calving and insect season) intervals and summarized over 24-h periods for analysis.

Relations between activity counts recorded by Wildlink collars and caribou behavior were evaluated using captive male and female caribou at LARS (Chapter 3). The "resting threshold" is a critical concept for the purposes of determining activity levels of radiocollared caribou. This threshold is defined as the sum of activity counts above which an animal is likely to have been active and was determined in each season, at a variety of activity levels of caribou (Fig. 14):

resting threshold = 0.20 * largest hourly activity count of the season.

The resting threshold was established to partition each 24-h period into resting and active bouts for each of the animals equipped with Wildlink collars. Thus, an active bout was defined as the sum of consecutive 1-h intervals during which activity counts

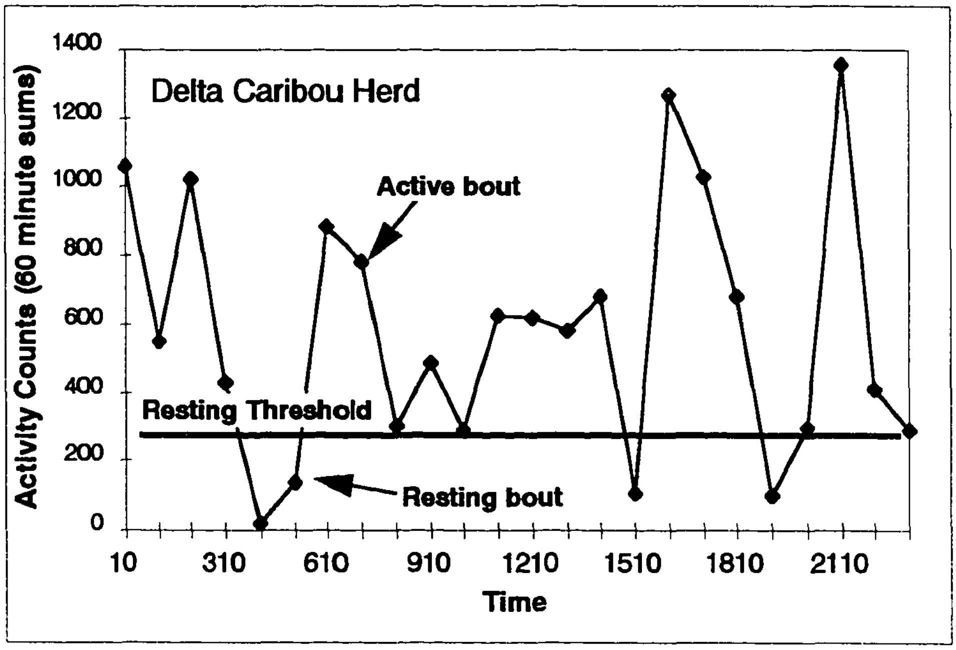

Fig. 14 Example of activity counts during a 24-hour cycle plotted vs. time of day for 1 adult (≥ 2 yr.) female caribou of the Delta herd in Alaska, 6 June 1991. Resting Threshold (RT) differentiates between active and resting bouts.

exceeded the resting threshold. The mean length of resting and active bouts per day was calculated from data on activity counts.

Caribou at LARS: To determine the baseline or typical seasonal patterns of activity for caribou, we collected activity data from six adult caribou (3 males, 3 females) at LARS during monthly, 24-h behavioral watches using focal-animal sampling (Altmann 1974). Behavioral categories included: lying with head down; lying with head up; standing; cratering; feeding; grazing; walking; running; sparring; playing; nursing; and attempted nursing. Temporal changes in activity over 30- or 60-min intervals were expressed as percent of time spent feeding. We used the resting threshold to categorize resting and active bouts and calculated the mean duration of these bouts.

Analyses

Mean durations of active and resting bouts are reported in minutes. Comparisons of mean duration of active and resting bouts were made between herds each season using one-way analysis of variance (ANOVA) in the winter and post-calving seasons. We used Scheffe's multiple comparison of mean effects to determine which effects were significantly different ($\alpha = 0.05$). In the insect season, comparisons were made between LARS and Delta herd caribou using t-tests. Statistical analyses follow Zar (1984). Significance was assessed at the 0.05 level.

Results

Forage quality and availability

Forage quality was high on ranges used by the Denali and Porcupine herds in winter and summer, moderate in winter and summer at LARS, and low on the range of the Delta Caribou Herd in winter, but unknown in summer (Table 2). Forage on range used by the Denali and Porcupine herds in winter included a high proportion of lichens (62% and 69% of the diet, respectively) and a low incidence of moss, graminoids, and woody shrubs (Table 3). Valkenburg (1994) documented that intake of moss was higher

Table 2. Qualitative descriptions of nutrition, snowcover, and insect harassment for caribou of the Large Animal Research Station (LARS), Delta Herd (Valkenburg 1994), Denali Herd (Boertje 1981, 1985), and Porcupine Herd (Russell et al. 1993) in late winter, during post-calving, and in the insect season, Alaska. Year = year of study.

	Range condition		Abiotic Factors	
Season/Herd	Quality	Availability	Snow depth/ Insects	Year
Winter				
LARS	Moderate	High	Shallow	1991
Delta	Low	Low	Deep	1991
Denali	High	High	Shallow	1978 - 80
Porcupine	High	Moderate	Variable, Deep	1979 &
Post-calving				
LARS	Moderate	High	-	1991
Delta	Unknown	Unknown	-	1991
Denali	High	High	-	1978 - 80
Porcupine	High	Moderate	-	1979 &
Insect				
LARS	Moderate	High	Low, mosquito	1991
Delta	Unknown	Unknown	High, flies	1991

Table 3. Percent of moss, graminoids, deciduous shrubs, and lichens in the diet of caribou in late winter. Moss, graminoids, and deciduous shrubs are associated with low quality winter forage of caribou in Alaska. Data are for the Large Animal Research Station (LARS), Delta Herd (Valkenburg 1994), Denali Herd (Boertje 1981, 1985), and Porcupine Herd (Russell et al. 1993) in late winter.

Herd	Moss	Graminoids	Deciduous shrubs	Lichens	Other
LARS	none	high	trace	none	high
Delta	34	2	11	48	5
Denali	10	11	<1	62	16
Porcupine	8	3	2	66	21

and intake of lichens was lower among caribou of the Delta herd than among any other herd in interior Alaska in winter (Table 3). Additionally, body weights of females in the Delta herd were declining in the years preceding this study (Fig. 13) and were at the lowest point in the year of the study (1991). Forage availability was high in all ranges except the Delta range, which was low (Table 2).

Forage quality on the ranges of post-calving Denali (Boertje 1981, 1985) and Porcupine (Russell et al. 1993) caribou was high (Tables 4a and 4b). Components of the diet selected by caribou of the Denali herd (Table 4a) and Porcupine herd (Table 4b) were high in chemical nutrients (nitrogen ranged from 2.7 to 4.8 g/100g DM in components selected most frequently) and contained moderate levels of fiber (ADF ranged from 12.6 to 15.5% in components selected most frequently). Both herds ingested a large amount of high quality deciduous shrubs (45% and 38%, respectively). Diets of Denali caribou consisted of 25% lichens, 16% forbs, 12% graminoids, and 2% berries, whereas Porcupine caribou selected a high proportion of forbs (32%), lichens (13%), and graminoids (8%; Table 4a and 4b). LARS caribou had access to ad libitum pellets, containing low-fiber (ADF) levels and moderate levels of nitrogen (2.9 g/100g DM), and a high-quality brome pasture (ADF levels = 28.9, N = 4.3; Table 4c). Forage quality and availability were unknown in the Delta caribou herd range during the post-calving period.

LARS caribou ingested higher levels of fiber (ADF = 46.5) and lower levels of nitrogen (2.8 g/100g DM) and phosphorous (0.2 g/100g DM) in the brome-hay pasture during the insect season. LARS caribou had ad libitum access to pelleted ration, however, consistent with availability and quality during the post-calving season. Forage quality and availability were unknown in the Delta caribou range during the insect season.

Environmental factors

Snow cover was low and not limiting on range used by Denali caribou (Boertje 1981, 1985) and variable, but deep on the winter ranges of the Porcupine Herd (Russell

Table 4. Nutrient analysis of vegetation (Vegtype) used by post-calving caribou at LARS, the Denali (Boertje 1981, 1985) and the Porcupine (Russell et al. 1993) caribou herds, in Alaska. QT = Quality Texture pelleted ration. Nutrients include fiber components: Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), Lignin, and Cellulose (cell wall content is reported in lieu of NDF for the Denali caribou herd). Chemical nutrients are Nitrogen (N) and Phosphorous (P) expressed as g/100g DM. ND = Not determined.

	Intake	Fiber				Nutrients	
Vegtype	% of diet	NDF	ADF	Lignin	Cellulose	N	P
a) LARS							
QT	unknown	ND	8.2	ND	ND	2.9	0.9
Pasture	unknown	ND	28.9	ND	ND	4.3	0.5
b) Denali							
Lichen	25	72.9	9.9	2.9	6.4	0.4	0.0
Graminoid	12	62.6	25.7	3.1	22.2	2.7	0.3
Deciduous	45	19.8	15.4	4.2	11.2	3.7	0.5
Forb	16	18.6	15.5	3.3	11.5	3.8	0.6
Berries	2	20.0	14.6	3.0	11.5	0.6	0.1
c) Porcupine							
Lichen	13	28.5	4.5	2.0	2.0	0.4	0.0
Graminoid	8	64.3	23.6	1.3	22.2	2.1	0.3
Deciduous	38	12.9	12.6	4.5	6.4	4.8	0.7
Forb	32	19.8	13.7	6.7	7.0	3.2	0.4
Evergreen	3	30.7	18.7	5.4	13.3	0.9	0.1
Moss	6						

et al. 1993) and Delta Herd (Table 2) during the years of the studies. Although LARS caribou were subjected to similar winter snow as the Delta Herd, food was ad libitum.

Insect harassment, an effect of summer weather, was low at LARS, and restricted largely to mosquitoes (Culicidae). Caribou at LARS were, on occasion, severely attacked by mosquitoes as determined by landing events on human observers and avoidance responses of caribou (frantic running and shaking of head, back, and rump). Nonetheless, insect harassment was generally low at LARS. Caribou in the Delta Herd exhibited avoidance behavior to oestrid flies (standing with head down, shaking their head; M. D. Smith, pers. comm.), suggesting they were subjected primarily to harassment by warble (Hypoderma tarandi) and nasal bot flies (Cephenemyia trompe) (Table 2).

Resting and Active Bouts

In late winter, lengths of active bouts were equivalent across groups (F = 0.25; df = 3, 32; $P = 0.86$), however, lengths of resting bouts differed significantly among groups (F = 4.78; df = 3, 32; $P = 0.007$). Mean length of resting bouts among the 4 groups of animals ranged from 137 (LARS caribou) to 227 minutes (Delta caribou) in late winter (Fig. 15b). Mean duration of active bouts during this season ranged from 145 minutes (Denali caribou) to 152 minutes (Porcupine and Delta Herds; Fig. 15a). Caribou at LARS were active, on average, for 149 minutes per bout in late winter.

Post-calving caribou of the Porcupine Herd exhibited significantly shorter resting bouts (83 min) than did LARS caribou (137 min) followed by those from the Denali (105 min) and Delta (125 min) herds (F = 4.27; df = 3, 121; $P = 0.02$) (Fig. 16b). Lengths of active bouts differed significantly among groups during post-calving (F = 13.89; df = 3, 96; $P = 0.027$). Caribou of the Denali Herd engaged in the shortest activity bouts (74 min) followed by those of the Porcupine (102 min), LARS (125 min), and Delta (205 min; Fig. 16a) herds.

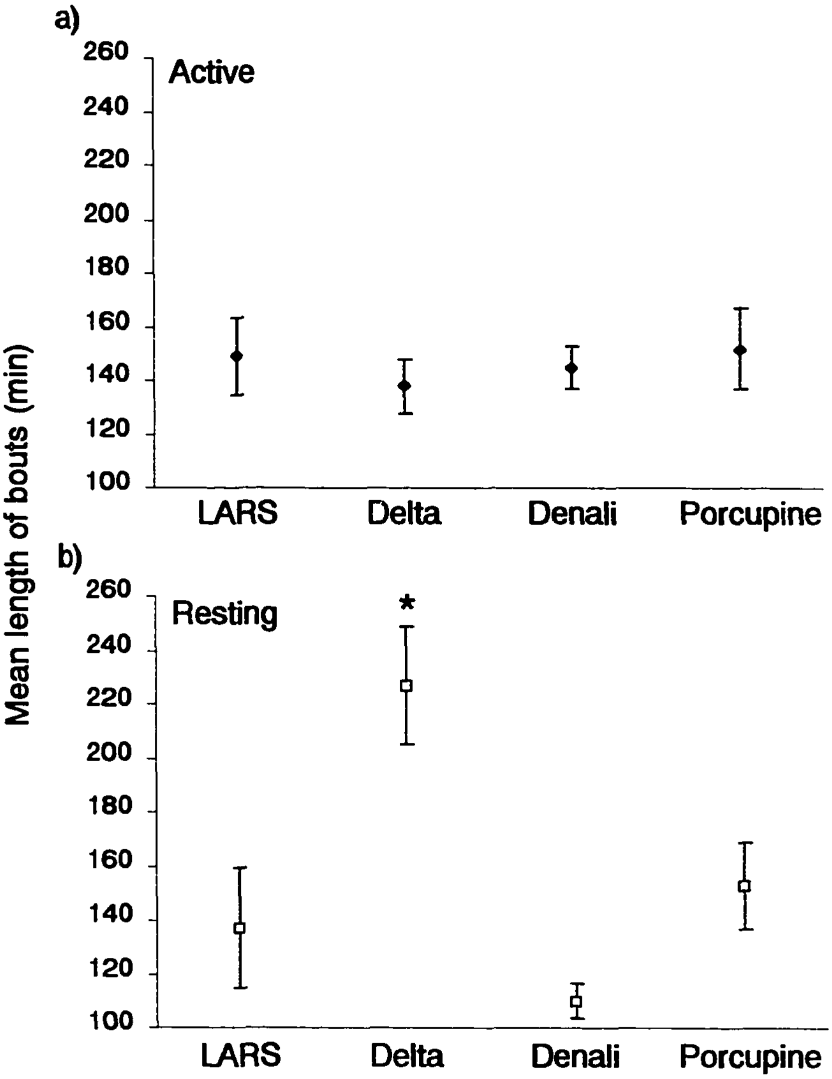

Fig. 15 Comparisons (ANOVA) of the mean length of a) active and b) resting bouts for caribou at LARS and caribou of the Delta, Denali (Boertje 1981), and Porcupine (Russell et al. 1993) herds for late winter in Alaska. An asterisk denotes a significant difference among the 4 herds ($p \leq 0.05$).

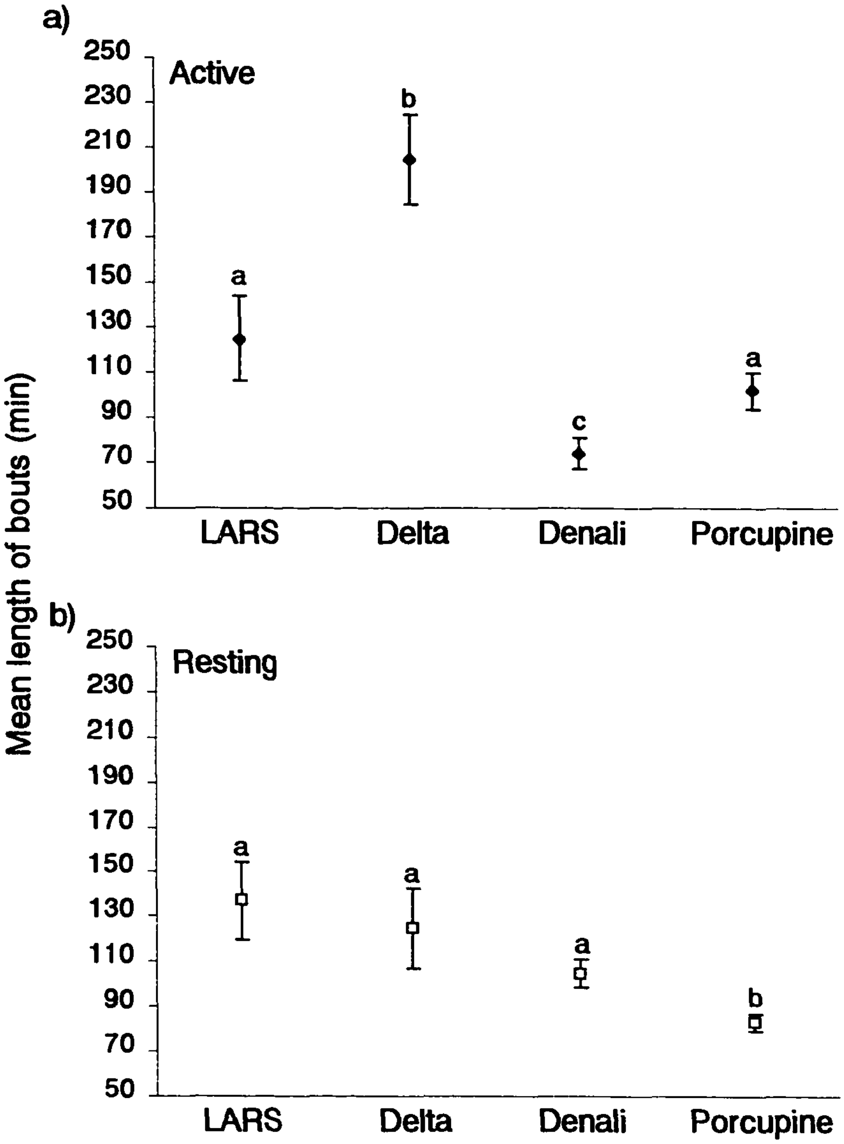

Fig. 16 Comparisons (ANOVA) of the mean length of a) active and b) resting bouts for caribou at LARS and caribou of the Delta, Denali (Boertje 1981), and Porcupine (Russell et al. 1993) herds for the post-calving season, Alaska. Means with different letters are significantly different ($p \leq 0.05$).

In the insect season, caribou of the Delta Herd exhibited shorter resting bouts than their counterparts at LARS (*P* = 0.01) and longer active bouts (273 min for Delta and 93 min for LARS caribou, respectively; Fig. 17; *P* = 0.0001).

Caribou at LARS exhibited comparable lengths of resting bouts across seasons (F = 0.21; df = 2, 35; *P* = 0.82). Active bout lengths were significantly shorter in the insect season than in late winter (F = 5.22; df = 2, 35; *P* = 0.01). Lengths of active bouts of the Delta caribou were significantly longer in the insect season than in late winter (F = 7.78; df = 2, 89; *P* = 0.0008). Correspondingly, Delta caribou exhibited longer resting bouts in late winter than in either the post-calving or the insect season (F = 18.17; df = 2, 89; *P* = 0.0001).

Discussion

Activity patterns of caribou reflect forage quality and forage availability, despite confounding interactions between these variables (Fig. 12) and abiotic and biotic environmental factors. In theory, lengths of resting bouts are driven primarily by forage quality but are negatively correlated both with forage quality and forage availability (Forchhammer 1995). Thus, an interaction occurs whereby ruminants make behavioral choices regarding retention time in an effort to increase nutrient digestion (Lundberg and Palo 1993; Forchhammer 1995). Using lengths of active bouts as indicators of range quality is problematic as lengths of active bouts seem virtually unaffected by changes in resource quality except when both quality and availability are low, resulting in long bouts of activity (Fig. 12a).

In the 2 seasons when comparisons were made across 4 herds of caribou, bout lengths were shortest when forage quality and availability was high, as expected (Fig 12). In late winter, caribou of the Delta herd exhibited long resting bouts (227 min) suggesting low quality and low availability of forage, which is supported by fecal-pellet analysis showing a high proportion of moss in their diets (Table 3; Valkenburg 1994). High-quality nutrition was correlated with short resting bouts in caribou of the Denali

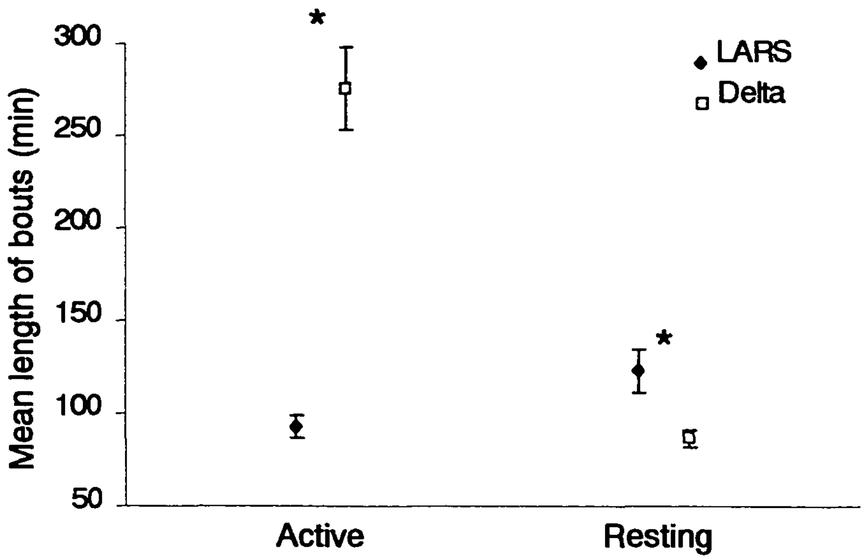

Fig. 17 Comparisons of the mean length of active and resting bouts for caribou at LARS and caribou of the Delta herd for the insect season, Alaska. An asterisk denotes a significant difference ($p \leq 0.05$) between LARS and Delta caribou.

Herd (110 min) in late winter. Caribou of the Porcupine Herd displayed relatively long resting bouts, possibly due to deep snow, despite high-quality nutrition (Tables 2 and 3; Russell et al. 1993). LARS caribou, with access to unlimited food of moderate-high digestibility and high crude protein, engaged in resting bouts of medium length (Tables 2 and 3, Fig. 15b).

In post-calving caribou, the shortest active bouts were exhibited by Denali caribou and were associated with high-quality, highly available forage (Table 2; Boertje 1981, 1985), whereas the longest active period for the Delta herd was indicative of low availability of food. These data support the hypothesis of a poor range that resulted in low growth of young animals (Fig. 13). The resting period for the Delta herd was intermediate in length (125 min), indicative of moderate to high quality forage. The short resting bouts, exhibited by post-calving animals of the Porcupine herd (Table 4b), was likely the result of high-quality, highly available forage as predicted from Fig. 12b, and supported by field evidence (Russell et al. 1993). LARS caribou displayed active and resting bouts of moderate lengths, yielding no predictive information regarding range quality (Tables 4c, Fig. 16); however, these results are associated with ad libitum food of moderate to high quality and should reflect time to process a maximum daily food intake.

Insect harassment may regulate the level of caribou activity during summer when foraging behavior is superseded by insect-avoidance activity. Although long active bouts may indicate forage of low quality and availability in the Delta herd (Fig. 12a), Delta caribou also exhibited short resting bouts, indicating forage of high quality but of unknown availability (Fig. 12b). These confounding effects are likely due to insect avoidance behavior of Delta caribou (Table 2). Harassment by insects causes caribou to display a longer amount of daily time spent active and a short daily time spent resting, as they choose to engage in avoidance behavior rather than foraging (White et al. 1975, Dau 1986, Nixon 1991, Russell et al. 1993). Therefore, in this instance, long active bouts are not related to forage availability. Furthermore, short resting bouts may not reflect high-quality forage because under conditions of intense insect harassment, caribou may interrupt lying bouts in response to insects (White et al. 1975, Dau 1986, Nixon 1991, Russell et al. 1993). LARS caribou displayed active bouts virtually equivalent to those recorded post-calving (Fig. 17) supporting our observations that insect harassment was absent at this time. Thus, the very short active and intermediate length resting bouts of LARS caribou most likely reflect forage of high quality and ad libitum availability, equivalent to good-quality resources in the wild.

Predation risk is a primary determinant of foraging behavior of some ungulates, including moose (Molvar and Bowyer 1994), and has been postulated as an important component in the foraging ecology of caribou (Bergerud 1980). Ungulates, which are vulnerable to predation, are constrained to forage in areas of low predator risk regardless of forage quality and availability (Edwards 1983, Festa-Bianchet 1988, Berger 1991). Caribou may respond to risk from mammalian predators by choosing low-risk areas, particularly during the calving season (Bergerud 1980, 1987; Bergerud et al. 1984; Skogland 1989; Adams et al. 1995). Nevertheless, caribou no longer modify foraging behavior in response to predation risk once caribou calves gain mobility (Skogland 1989). Further, Post (1995) noted that caribou did not modify foraging behavior in response to the presence of predators and concluded that caribou restricted themselves to more immediate responses to predation, such as flight. Although caribou apparently are not regulated by predation (Dale et al. 1994) except, perhaps, when they occur at low population densities, the predation-sensitive food hypothesis has not been tested adequately for this ungulate. Sinclair and Arcese (1995) documented joint regulation of wildebeest (Connochaetes taurinus), an ungulate quite similar to caribou in terms of life-history strategies (e.g., social foraging, migration, open environments), by food and predation. Caribou, like wildebeest, likely are subjected to areas of variable forage quality and availability and fluctuating predation risk, despite persistence in relatively homogenous environments. Within the constraints of high population density, caribou may have to make choices regarding forage quality versus increased predation risk to maximize body condition and individual fitness. Hence, predators may affect foraging decisions and, in turn, activity of caribou. We did not measure, nor do we know, the predation effects on activity of caribou in our study.

The relation between range quality and caribou activity is complicated by extreme weather (Skogland 1984, 1989). In winters characterized by deep snow, caribou may conserve energy by lying rather than searching for food, a time-minimizing strategy, thereby increasing the duration of resting bouts (Russell and Martell 1984, 1986; Roby and Thing 1985; Skogland 1984, 1989). In this instance, long resting bouts are indicative of low availability of forage, independent of quality. Alternatively, caribou may respond to deep snow by becoming less selective, again increasing the length of resting bouts as it takes more time to digest poor quality forage. This strategy was evidenced in Delta Herd caribou seen foraging on willow (Salix) stems in late winter. Moreover, the energetic cost of traveling and cratering through deep snow may result in increased lying, regardless of forage availability or quality. We suggest the long resting bouts noted in the Delta caribou herd in late winter could be an example of a time-minimizing strategy in response to deep snow (Tables 2, Fig. 15b), likely a combination of factors including less-selective foraging, and, correspondingly, increased rumination time, and an energy-conservation strategy of increased resting (nonruminating). Caribou of the Porcupine Herd displayed relatively long resting bouts, despite moderate-quality nutrition, which also may reflect deep snow (Tables 2, Fig. 15b). Caribou of the Porcupine Herd, however, exhibited substantially shorter resting bouts than their Delta caribou counterparts, also were subjected to deep snow. The difference in resting-bout lengths between these 2 populations is likely due to nutrition (Table 3) or possibly snow characteristics other than snow depth, which was approximately equivalent (maximum snow depth was 104 cm in the Delta Herd range and 92 cm in the Porcupine range).

Activity of caribou also may reflect body condition in winter. Those in poor condition show an increased time spent lying (Roby 1980, Roby and Thing 1985), a time-minimizing strategy used when resource quality is low as in West Greenland. Caribou in poor condition should increase feeding time unless forage is of low quality or is unavailable because of over-grazing, deep snow, or other natural phenomena (e.g., habitat destruction by fire; Klein 1982, Russell et al. 1993).

The concept of using bout lengths as an index of range quality is further complicated by the host of possible responses to resource limitation. Foraging effort of caribou increases as food density decreases within a season, thus resulting in longer periods of activity (Trudell and White 1981, Spalinger et al. 1988). Caribou, however, may become less selective or choose more favorable food patches, if they are available, under the scenario of resource limitation (Charnov 1976, Charnov et al. 1976, Parker 1984, Stephens and Krebs 1986). In either instance, lower forage availability will not necessarily result in increased length of active bouts (Fig. 12a). Low availability of forage may, however, result in longer resting bouts as caribou seek to extract the maximum amount of nutrients from scarce forage (Lundberg and Palo 1993, Forchhammer 1995). Alternatively, foraging effort decreases as food density increases, to the extent that forage availability no longer limits intake (Trudell and White 1981, Spalinger et al. 1988). Thus, no change in length of active bouts would be detected with increased forage availability.

Theoretically, lengths of resting and active bouts interact with resource quality resulting in daily feeding times that are negatively correlated with forage quality and which are unrelated to forage availability (Fig. 12d; and Forchhammer 1995, Forchhammer and Boomsma 1995). This result is due both to the distribution of resources and the need of the animal to ingest a variety of forage types (White 1983). The necessity of foragers to move from one patch to another is minimized in a homogenous environment where high-quality forage is available in large quantities (Parker 1984, Stephens and Krebs 1986). Accordingly, length of active bouts surely reflects resource availability. Daily feeding times, however, might not reflect resource availability as the animal still has to fulfill nutritional requirements resulting in longer feeding times than expected, notwithstanding high availability of forage.

Conclusions

Some differences between caribou populations, within a season, are evident. In late winter, there are no differences in active bout lengths among groups, despite a wide range of forage availability (Tables 2 and 3), supporting the theory that length of activity bouts are less sensitive as a measure of resource quality (Fig. 12a). Because resting bouts are significantly longer than for the other groups of caribou in winter we conclude that Delta caribou are subjected to both low quality and low availability range.

In post-calving caribou, the short resting bouts (83 min) exhibited by Porcupine caribou are likely due to high-quality, highly available forage, supported also by a moderately short active period. Although a short active period is not definitive for determining the relative contribution of quality and availability of forage, the moderately short resting periods of Denali caribou imply a good range. Delta caribou exhibited significantly longer active bouts, suggesting forage was of low availability. Resting bout lengths exhibited by caribou of the Delta herd were equivalent to LARS and Denali caribou indicating comparable quality of forage among these herds.

In the insect season, the short resting bouts (86 min; $P = 0.01$) of Delta Herd caribou suggest a high-quality range. This herd also engaged in extraordinarily long active bouts (273 min; $P = 0.0001$), however, which strongly supports field observations of high levels of insect harassment. Insect harassment is the likely cause of both the long active and short resting bouts of the Delta herd in that season.

CHAPTER 3: RESPONSES OF CARIBOU TO LOW-ALTITUDE JET AIRCRAFT OVERFLIGHTS[3]

Abstract: Military training exercises have increased in Alaska in recent years and the possible effects of low-altitude overflights on wildlife, such as caribou (Rangifer tarandus), have caused concern among northern residents and resource agencies. We evaluated the effects of overflights by low-altitude, subsonic jet aircraft by U. S. Air Force A-10, F-15, and F-16 jets on daily activity and movements of free-ranging female caribou. This study was conducted on caribou of the Delta Caribou Herd in interior Alaska in each of 3 seasons in 1991: late winter, post-calving, and insect harassment. We measured activity using activity monitoring radiocollars (Wildlink, Inc.) and calculated movements from daily relocations. Noise levels experienced by caribou were measured using Animal Noise Monitors (ANMs) that were attached to the Wildlink radiocollars. Caribou subjected to overflights in late winter responded by interrupting resting bouts and, thus, engaged in a greater number of resting bouts than caribou that were not subjected to overflights. Caribou subjected to overflights during post-calving were more active and moved farther than did caribou that were not subjected to overflights. Finally, caribou subjected to overflights during the insect season responded by becoming more active. Responses of caribou to aircraft were mild in late winter, intermediate in the insect season, and strongest during post-calving. We conclude that females with young are more sensitive to aircraft disturbance. Accordingly, curtailment of military training exercises in areas where caribou are concentrated should be a priority during calving and post-calving.

Key words: activity, aircraft, Alaska, caribou, movement, noise, Rangifer tarandus.

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[3] Maier, J. A. K., Murphy, S. M., White, R. G., and Smith, M. D. In Prep. Responses of caribou to low-altitude jet aircraft overflights. J. Wildl. Manage. 00:000-000.

Introduction

As habitat availability decreases and wildlife populations decline, the effects of human disturbance on these limited resources becomes critical. Resource-management agencies have been addressing the issue of anthropogenic disturbance on wildlife and habitat for many years and have identified a variety of problems regarding aircraft disturbance, including: flushing of birds from nests or feeding areas (Owens 1977, Kushlan 1979, Burger 1981, Anderson et al. 1989, Belanger and Berad 1989), alteration of movement and activity patterns of mountain sheep (Ovis canadensis) (Bleich et al. 1990, 1994), decreased foraging efficiency of desert bighorn sheep (Stockwell et al. 1991), panic running by barren-ground caribou (Rangifer tarandus) (Calef et al. 1976), decreased calf survival of woodland caribou (Harrington and Veitch 1992), and increased heart rate in elk (Cervus elaphus), antelope (Antilocapra americana), and rocky mountain bighorn sheep (Bunch and Workman 1993). With expansion of residential and industrial development, habitat for animal populations becomes limited and open country suitable for military-training exercises decreases. Vast tracts of uninhabited land in Alaska makes this state an attractive location for increasing the range and intensity of military training exercises as well as the long-term designation of such tracts of land for military use. Military-training exercises have increased in Alaska in recent years by 33% and the postulated effects of low-altitude overflights by jet aircraft on wildlife, such as caribou, have caused concern among northern residents and resource management agencies.

In response to these concerns, the U.S. Air Force (USAF) initiated a number of research projects throughout the U.S. to better understand the effects of their training exercises on a variety of wildlife species. Caribou were selected for this study primarily because detailed models of their energetics were available, because the Delta Herd in interior Alaska occurs near Eielson Air Force Base, and because this area has been used traditionally by the USAF for jet-training exercises. The goal of this research was to quantify long-term responses of caribou to overflights by sub-sonic jet aircraft flying at altitudes as low as 33 m above ground level (agl). Our specific objectives were to: (1) measure the noise exposure experienced by caribou overflown by jet aircraft; (2)

determine activity cycles and movements of caribou exposed to overflights by low-altitude jet aircraft using telemetry; and (3) evaluate responses of caribou to overflights as a function of noise exposure. We predicted that caribou exposed to overflights by jet aircraft would engage in longer periods of activity, shorter periods of resting, and would travel farther than caribou that were not subjected to low-altitude overflights by military jet aircraft.

Disturbance by aircraft may result in a variety of effects on ungulates, including movement from the area of disturbance and changes in habitat use seen in mountain sheep (Krausman and Hervert 1983, Krausman et al. 1986, Bleich et al. 1990, 1994), decreased frequency of nursing in caribou (Gunn et al. 1985), increases in heart rate in mountain sheep (MacArthur et al. 1979, 1982; Krausman et al. 1993; Weisenberger et al. 1996) and desert mule deer (Odocoileus hemionus) (Weisenberger et al. 1996), and overt behavioral responses in caribou (Harrington and Veitch 1991).

Studies by Harrington and Veitch (1991, 1992) have particular relevance to this study. These authors noted that female caribou exposed to low-altitude overflights by jet aircraft had lower survival of their calves than female caribou that were not subjected to this disturbance. In contrast, Valkenburg and Davis (1985) concluded that caribou of the Delta Herd are habituated to aircraft disturbance and that, disturbance had not adversely affected productivity, until at least 1984 (Davis et al. 1985), even though the Delta Herd had been exposed to frequent low-altitude overflights by military and civilian aircraft for a number of years (more than any herd in Alaska). These conclusions, however, were based on annual trends in productivity of the Delta Herd, compared with other herds in Alaska that were not exposed to low-altitude overflights by military aircraft, rather than by any actual evaluation of the effects of overflights on individual animals.

Study area

There were three separate periods of field activity for this project: late winter (30 March - 6 April 1991), post-calving (7-16 June 1991), and the insect harassment season (26 July - 3 August 1991). During the week prior to each sampling period, reconnaissance surveys were flown to determine where the caribou of the Delta Herd were distributed over its 9,600 km^2 range (Davis et al. 1985). Animals that had been radiocollared previously by the Alaska Department of Fish and Game (ADFG) were located and a general impression of herd distribution was ascertained. A study area and a location for our field camp then was selected based on the distribution of caribou and logistical considerations. Locations of the study areas differed among sampling periods, but always were located on the north side of the central Alaska Range (64°14'N, 148°34'W; 63°35'N, 146°14'W; Fig. 18).

The range of the Delta Herd is physiographically diverse with rugged, glaciated peaks and ridges (1500 to 3500 m elevation) to the north and the Tanana Flats lowland (150 to 600 m) to the south. Foothills (1000 to 1500 m) rise from the Tanana lowlands and it is here that the Delta Herd spends much of its time. The foothills are dissected by northward-flowing glacial streams and steep-sided valleys. Timberline is located between 600 and 800 m; forest vegetation predominates in the Tanana lowlands and tundra in the foothills. Dominant species of tree are white and black spruce (Picea glauca, P. mariana), paper birch (Betula papyrifera), and quaking aspen (Populus tremuloides) (Fleischman 1990). Tundra communities are dominated by shrub birch (Betula glandulosa), willow (Salix sp.), ericaceous shrubs, sedges (Carex sp., Eriophorum sp.), mosses, and lichens (Fleischman 1990).

Methods

For each sampling period, we captured and instrumented caribou with radiocollars and noise monitors prior to the onset of data collection. A team of 3 scientists, using both helicopter and fixed-wing aircraft, flew to the designated study area at least 2 days prior to the beginning of the overflights and captured and instrumented 2 groups of up to 5 adult (≥ 2 years of age) female caribou by darting them from a helicopter. Darts contained a mixture of carfentanil (0.036 mg/kg body weight) and 100 mg xylazine.

One group of 5 caribou, the treatment group, was designated to be overflown by jet aircraft. Five other animals, the control group, were captured at least 16 km from the

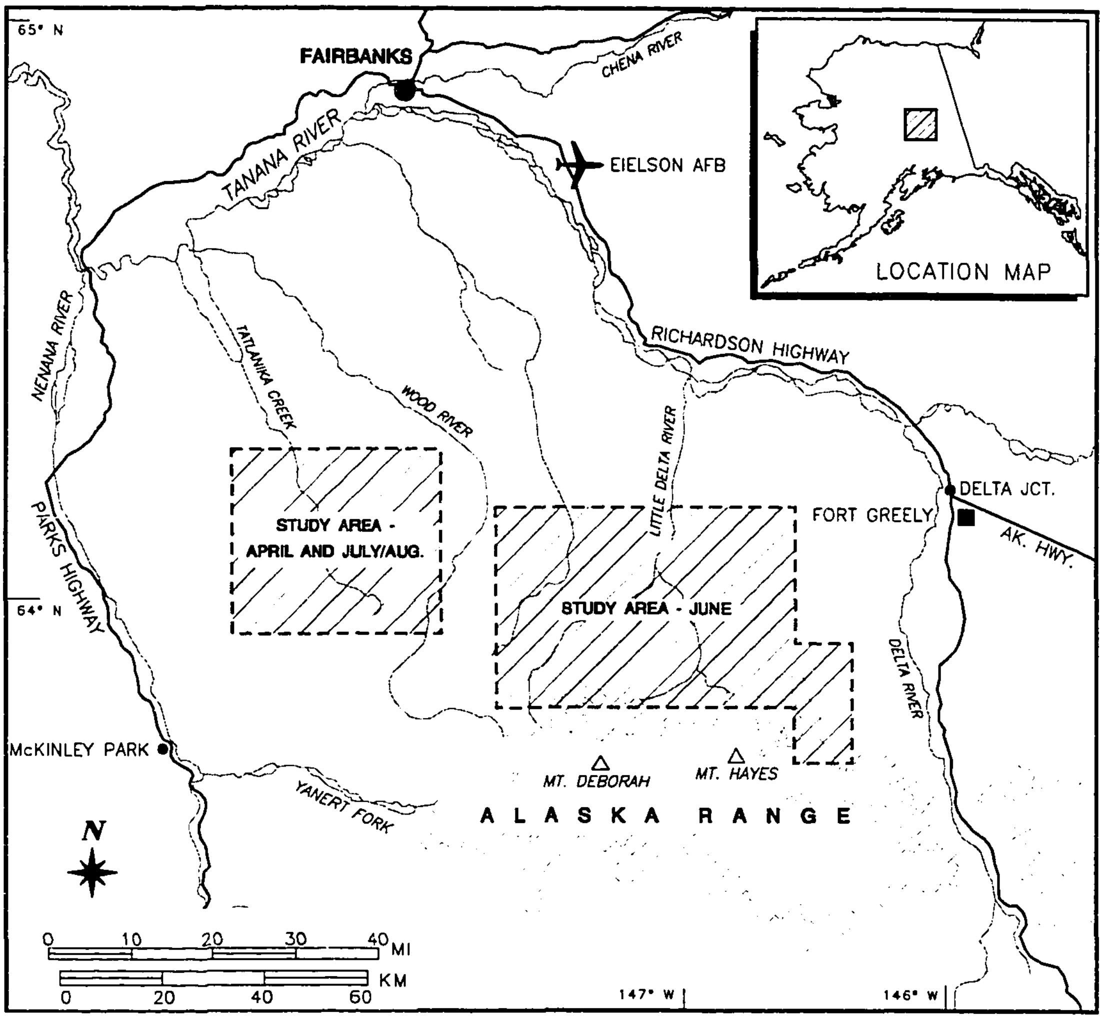

Fig. 18 Location of study areas in Alaska used to observe the effects of low-altitude overflights by military jet aircraft on caribou, 1991.

treatment group and were designated to not be exposed to overflights. All captured animals were instrumented with Wildlink radiocollars (Wildlink, Inc., ® St. Paul, MN, 55444) that were equipped with VHF radio transmitters and an activity counter. The 5 animals in the treatment group also were outfitted with Animal Noise Monitors (ANMs; Murphy et al. 1993). Each ANM was protected by a cordura pouch with an aperture for a microphone. The pouches were affixed to the top of Wildlink collars so that the microphones would be exposed directly to the noise from aircraft. After collaring, caribou were given an intramuscular injection of penicillin (100 mg), a topical application of antibiotic powder, and the reversing agents naloxone (150 mg naloxone/mg carfentanil) and yohimbine (0.2 mg/kg body weight). Caribou were given ≥ 4 days to recover before data collection ensued. Presumably, a 4 day period of recovery was adequate because collared caribou behaved analogously to uncollared caribou prior to and after the overflight period (determined from activity budgets of collared and uncollared caribou located in the same group). Collars were retrieved at the completion of each sampling period.

Days scheduled for overflights began with a radiotracking flight to locate all of the instrumented animals in the treatment group. A team of biologists and an air controller began observations of one of the treatment caribou. The animal was selected based upon availability to the observation team and accessibility by jet aircraft (e.g., animals located in box canyons were avoided). Once on site, the air controller installed the radio equipment and waited to hear from USAF pilots in the vicinity. After radio contact was established, the air controller notified the pilots of the location of treatment caribou and then directed the jets along specific flight paths requested by the biologists. In most instances, the pilots were directed to fly directly over the caribou at 33 m above the ground at high or full power settings. Pilots also were instructed to maintain at least 5 min intervals between multiple overflights.

Noise Exposure

Noise generated by jet aircraft was measured using prototype ANMs and stationary acoustical noise monitors. Because the primary objective for noise monitoring was to measure noise exposure experienced by caribou overflown by jet aircraft, we designed equipment capable of accurately measuring noise exposure for free-ranging animals. The prototype ANMs were developed specifically for this program and represent the first time that a measurement of noise exposure was made on free-ranging animals in their natural habitats. Murphy et al. (1993) provides a detailed description of the ANMs.

ANMs measure and calculate a number of acoustic variables, such as a Maximum Noise Level (L_{max}) and Sound Exposure Level (SEL), using both A- and C-weighted scales (American National Standards Institute 1990). This information, together with date, time, and some data on activity, was stored in the ANM memory.

During late-winter, two ANMs were programmed with a noise-event threshold of 90 dBA, which had to be exceeded for > 2 seconds to be activated, and three ANMs were programmed with a noise-event threshold of 85 dBA, which had to be exceeded for > 2 seconds for activation to occur. During the insect season and post-calving period, all ANMs were programmed to record all noise events that exceeded 85 dBA for > 2 seconds.

SEL is a measure of the total amount of acoustical energy generated during an event calculated by logarithmically integrating the magnitude of sound over the time period of that event. A-weighted SEL in decibels (dBA) was the noise descriptor selected for analysis of the noise "dose" received by the caribou. For each aircraft overflight, the SELs measured by the ANMs were used to describe the noise exposure of each individual or groups of caribou that contained instrumented animals. For caribou for which noise measurements from ANMs were not available, the OMEGA 14.6 Aircraft Noise Prediction Program developed by the USAF Occupational Environmental Directorate Bioenvironmental Engineering Division, Noise Effects Branch (AL/OEBN) was used to estimate the SEL. Variables required to estimate SEL using this program included aircraft type, number of aircraft, flight speed, power setting, and slant range (i.e., line of sight distance) from the aircraft to the caribou. Slant ranges calculated for animals that were not directly observed may have been inaccurate because of differences in the time when telemetry location was fixed and when overflights occurred. SELs were measured 58% of the time, using ANMs, across all seasons and were estimated (42% across all seasons) for each control animal and for treatment animals when ANMs failed.

Prior to analysis, SELs were adjusted using correction factors that were calculated for each season and type of aircraft. These correction factors were determined by averaging the difference between estimated and ANM-based measurements for individual overflights. A time-averaged sound level (L_T) was calculated to estimate daily noise exposure for each animal using the formula:

$$L_T = 10\log_{10}\left[\frac{1}{T}\sum_{i=1}^{N} 10^{SEL_i/10}\right],$$

where SEL_i is the Sound Exposure Level of the *i*th event in a series of *N* events over the time period *T* (American National Standards Institute 1990). L_T, the number of overflights > 85 dBA and ≤ 1 km, and the loudest overflight of the day were determined for each treatment animal for each day and used as independent variables in regression analyses.

Activity Cycles

The Wildlink collars were programmed to record and sum activity at 60-min intervals. Activity was recorded by a mercury tip-switch that registered a count (i.e., activity count) each time the collar was tilted. These collars, which can store up to 36 intervals of activity, were interrogated remotely from a fixed-wing aircraft every 18 h during late winter and every 24-h during post-calving and insect seasons. A triggering signal activated the collar, which responded by transmitting stored data (i.e. activity counts) in an audio binary code. The binary code was received using a Telonics receiver, recorded by hand, and later translated into Arabic numerals (Mech et al. 1990, Kunkel et al. 1991, Maier et al. 1996). Locations of collared caribou were recorded on 1:63,000 topographic maps each time activity data were downloaded. Accuracy of locations was not assessed but was surmised to be constant and unbiased across groups.

Three of nine VHF transmitters malfunctioned during late-winter leaving 5 animals in the treatment group, but only 1 animal in the control group. Nine collars were deployed during the insect season, 4 on animals in the treatment group and 5 on animals in the control group. One collar on an animal in the control group failed 3 days after the start of the sampling period, and another control animal wandered out of range and was not relocated until 3 days before the end of the sampling period; these animals were not used in analyses. Ten collars were deployed during post-calving; 3 of 5 caribou in the control group wandered into the treatment area and were exposed to overflights by low-altitude jet aircraft. Thus, 8 animals were overflown and only 2 animals were not exposed to overflights during this sampling period.

Activity-monitoring systems based on tip-switch technology are not capable of discriminating between specific activities (e.g., standing, feeding, walking). They are, however, capable of accurately depicting active and resting bouts, and these were recorded in 0.5-hour (late-winter) or 1-hour (post-calving and insect season) intervals. These data then were summarized over 24-h periods for analysis. During late winter, data only could be summarized over a 21-h period because of gaps in downloading of data in the field.

The relationship between activity counts recorded by Wildlink collars and caribou behavior was evaluated using captive male and female caribou at the Large Animal Research Station, Institute of Arctic Biology, University of Alaska Fairbanks. Data in Chapter 4 documented close agreement between activity counts, energy expenditure, and observed activity of captive caribou. Equations developed from this work on captive animals were used to interpret activity counts collected on wild caribou. Of specific importance to the results presented in this paper is the concept of "resting threshold"

(Chapter 2). The "resting threshold" was defined as the activity count sum above which an animal was likely to have been active:

resting threshold = 0.20 * largest hourly activity count of the season.

Outliers were removed based on the leverage technique whereby influential points were removed when they had ≥ 2.5 times the leverage of the average point (Neter et al. 1990). The resting threshold was established to partition each 24-h period into resting and active bouts for each of the animals equipped with Wildlink collars. Thus, an active bout was defined as the sum of consecutive 1-h intervals during which activity counts exceeded the resting threshold. The number of resting and active bouts, the mean length of resting and active bouts, and the daily time spent resting and active were calculated for each day. For comparisons of treatment and control animals, daily counts of activity were standardized to the proportion of total counts per season (i.e., daily activity counts / total counts per season) because of suspected among-collar variability.

Activity cycles were analyzed by comparing treatment and control groups and by multiple-regression analysis for treatment animals. Comparisons of treatment and control groups were made after verifying that individual animals actually had been overflown on a particular day. For example, if an animal from the control group moved into the overflight zone and was exposed to overflights ≥ 85 dBA, it was classified as a "treatment" animal for that day (this occurred 11 times, 10 during the post-calving period). Conversely, if an animal from the treatment group was not exposed to overflights on a particular day, it was classified as a "control" animal for that day (this occurred frequently because there were numerous days with no overflights). Comparisons between treatment and control groups were made for number of active and resting bouts per day, mean length of active and resting bouts, daily time spent active and resting, and proportion of total counts per season. ANOVA was used for these comparisons, and significance was assessed at $\alpha = 0.05$.

Movements

Locations of instrumented caribou and caribou under direct observation, together with the route of each overflight were plotted on digitized study area maps using Atlas GIS (Geographical Information System) software (Fig. 19). Error associated with flight paths was not assessed but was surmised to be constant and unbiased. Spatial analyses were performed to determine the distance traveled between daily locations for each animal, and the slant range from each instrumented caribou to each overflight route. That is, a linear, two-dimensional distance between telemetry locations recorded at 24-h intervals was calculated for both treatment and control animals.

Daily distance traveled by caribou was compared (one-way ANOVA) between treatment and control animals using the same criteria described previously to assign animals to the two groups (i.e., at least one overflight $\geq$ 85 dBA on a particular day for inclusion in the treatment group). Daily distance traveled was not normally distributed and, therefore, was ranked prior to statistical analyses (Conover 1980).

Regression Models

We evaluated whether specific aspects of noise could be identified as influencing activity cycles and daily movements of caribou using stepwise multiple regression (SAS1). Specifically, we attempted to determine which noise variables, if any, were related to variations in: (1) number of daily resting bouts; (2) mean length of resting bouts; (3) daily time spent resting; and (4) daily distance moved. The independent variables considered were: (1) number of overflights $\geq$ 85 dBA and $\leq$ 1 km; (2) loudest overflight each day; and (3) time-averaged noise exposure level for the treatment day (L_T). We determined the extent of collinearity among the independent variables using a correlation matrix. Only variables associated with resting were considered, because they essentially are the reciprocal of the active variables and because time spent resting per day was the primary variable used in modeling the population-level effects of overflights by low-altitude jet aircraft on caribou.

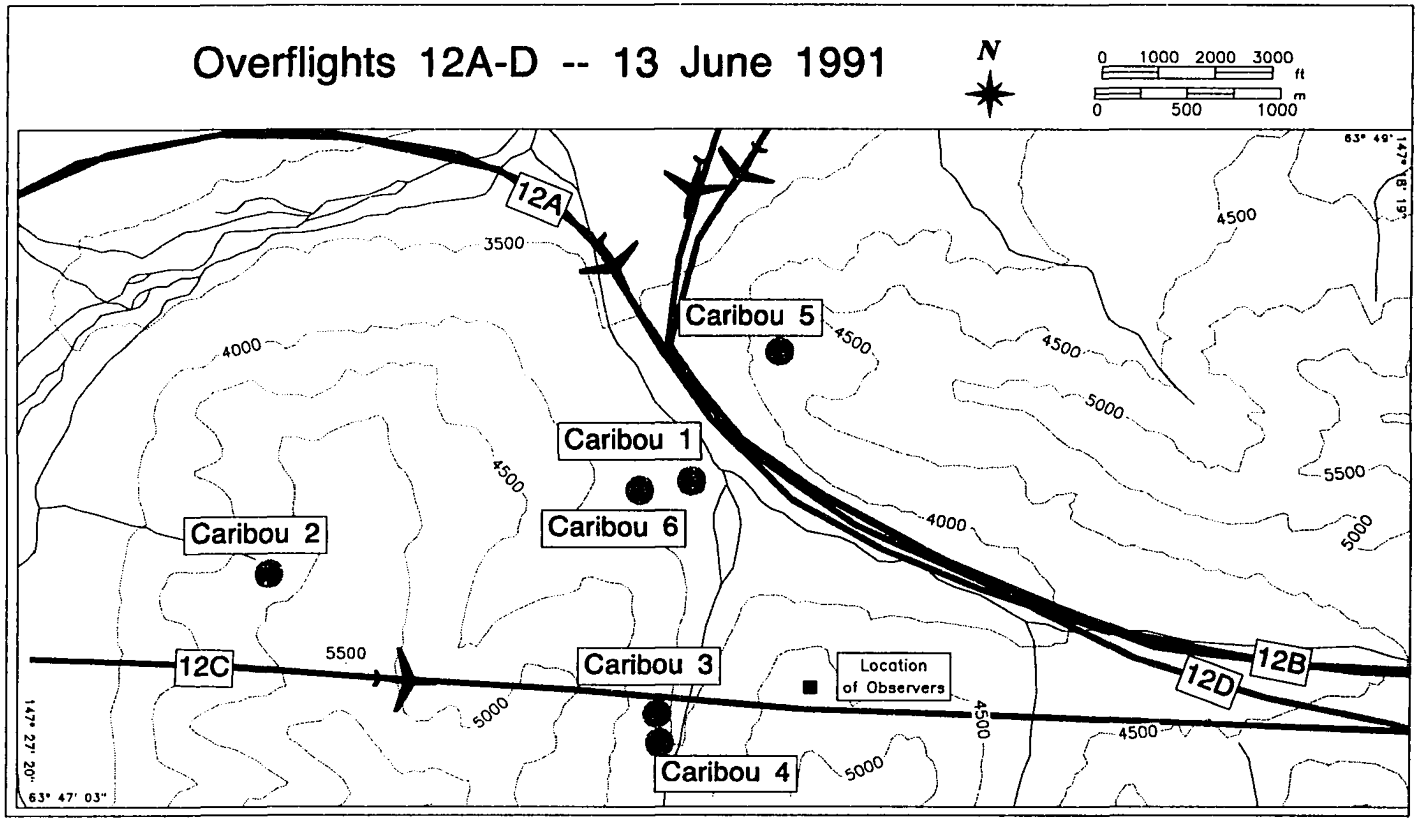

Fig. 19 Example of GIS output depicting locations of the observation team, collared caribou, and flight paths (12A, 12B, 12C, and 12D) of military jets in Alaska, 1991.

Results

Noise Exposure

Caribou were exposed to 159 overflights by jet aircraft during the 3 sampling periods. Of these jets, 94 were A-10s, 61 were F-15s, and 4 were F-16s. During late-winter and post-calving periods, only A-10 and F-15 aircraft were available, whereas all 3 aircraft were used during the insect season. Several groups often were observed simultaneously during overflights; therefore, 268 groups of caribou were observed during the 159 overflights.

Sound exposure levels (SELs) were measured or estimated for each overflight. For animals under direct observation, SELs ranged from 46 to 127 dBA; the maximum noise exposure was produced by an F-15 flying at a slant distance of 106 m from the caribou. The mean SEL for all 159 overflights was 98 dBA (Table 5). F-15s produced the greatest SELs (mean = 103 dBA), followed by F-16s (mean = 96 dBA) and A-10s (mean = 95 dBA). Most (> 70%) overflights that we observed resulted in SELs between 80 and 100 dBA. Forty-four percent of the overflights were in the 90 to 100 dBA range; < 10% of the overflights exceeded 110 dBA.

Activity Cycles

The number of resting bouts per day for animals in the control group ranged from 3.5 to 4.2 during the three sampling periods (Fig. 20a). Caribou in the treatment group had significantly more ($P = 0.05$) resting bouts per day during late winter than did caribou in the control group, whereas there were no differences during the other two sampling periods (Fig. 20a). The number of active bouts per day for animals in the control group ranged from 3.8 to 4.8 (Fig. 20b). Number of active bouts recorded for animals in the treatment group did not differ during any of the sampling periods (Fig. 20b).

The mean length of resting bouts for animals in the control group ranged from 1.4 to 3.8 h during the three sampling periods (Fig. 21a). Mean length of resting bout during the insect season for animals from the treatment group was significantly ($P = 0.02$)

Table 5. **Flight characteristics and estimated Sound Exposure Levels (SEL) of low-altitude overflights of caribou by military jet aircraft in Alaska, 1991.** ***n*** **= number of caribou groups (≥ 1 caribou) subjected to overflights.**

		Slant Distance (m)		Airspeed (km/h)		SEL (dBA)		
Aircraft	Season	Mean	SE	Mean	SE	Mean	SE	*n*
A-10	Late winter	375	28.4	470	3.8	99	1.1	77
	Post-calving	448	55.0	530	7.8	94	1.0	66
	Insect	749	221.9	526	12.0	90	2.5	24
	All	457	101.8	501	7.9	95	1.5	167
F-15	Late winter	538	76.4	659	23.6	106	2.3	28
	Post-calving	1606	330.5	560	50.4	96	1.1	27
	Insect	1414	308.3	693	8.9	105	2.0	34
	All	1197	238.4	642	27.6	103	1.8	89
F-16	Insect	1647	244.7	807	22.0	96	3.0	12
All		756	180.7	562	18.3	98	1.8	268

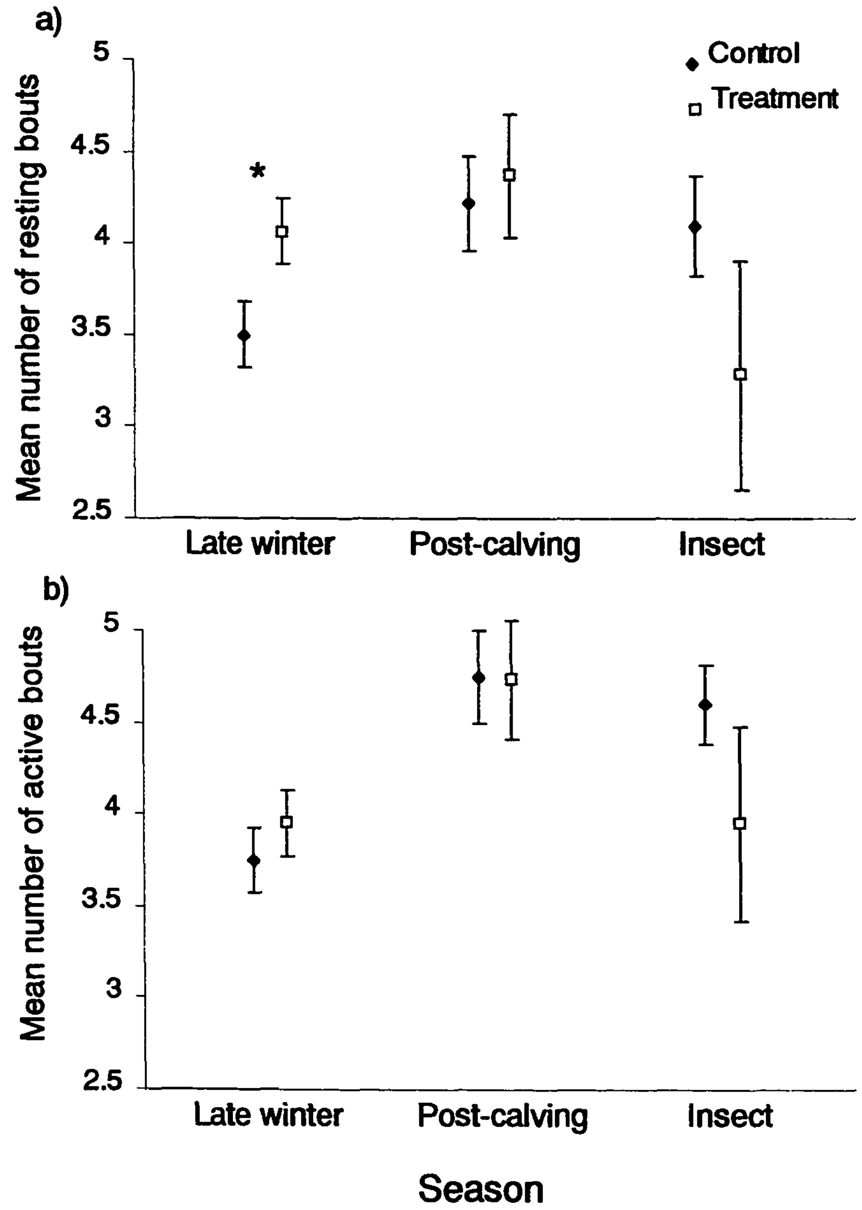

Fig. 20 Comparisons (ANOVA) of daily number of a) resting and b) active bouts for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. An asterisk denotes a significant difference between control and treatment groups ($p \leq 0.05$).

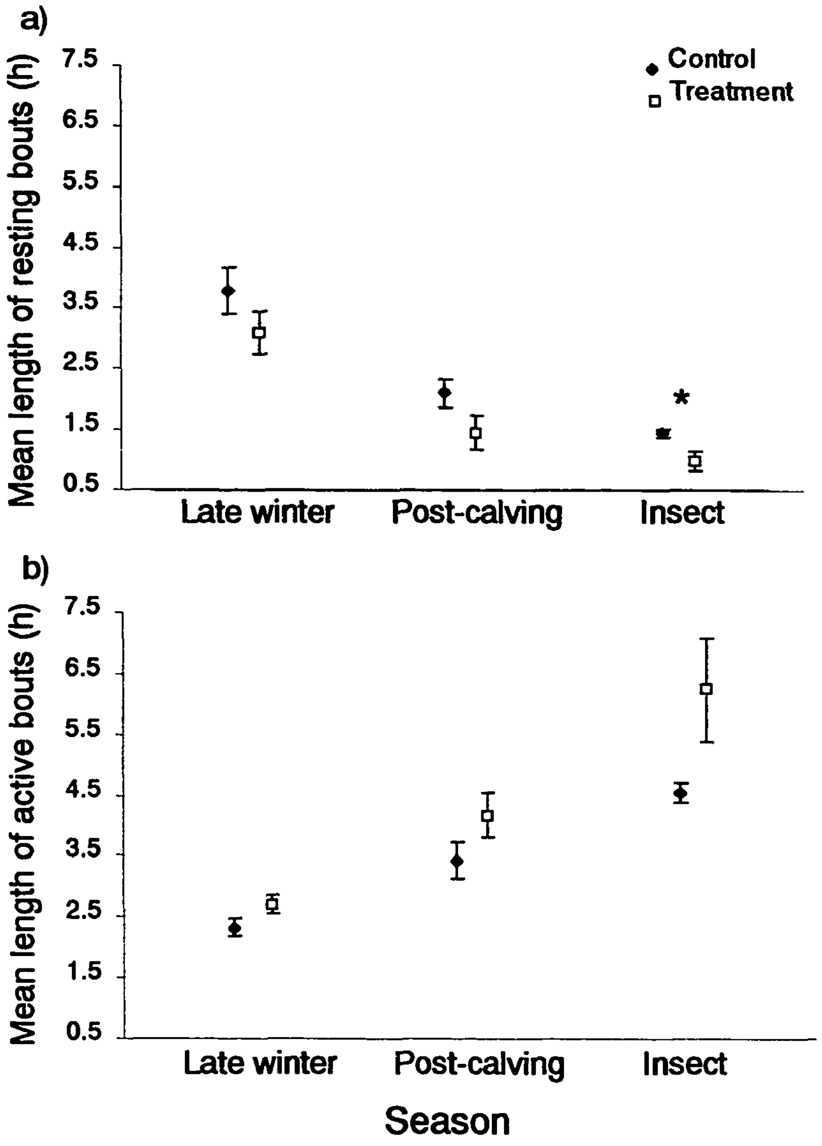

Fig. 21 Comparison (ANOVA) of the mean length of a) resting and b) active bouts for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. An asterisk denotes a significant difference between control and treatment groups ($p \leq 0.05$).

shorter than that of the control group (Fig. 21a). Despite a similar trend, there were no significant differences during the other two sampling periods. The mean length of active bouts for animals in the control group ranged from 2.3 to 4.6 h (Fig. 21b). Mean length of active bouts recorded for animals in the treatment group did not differ (*P* = 0.08) during any of the sampling periods, although there was a consistent trend for animals in the treatment group to have longer active bouts than animals in the control group (Fig. 21b). Both treatment and control animals had longer active bouts during the insect season than during the other two sampling periods, with an extreme value of 6.2 h of activity for treatment animals.

Daily time spent resting for animals in the control group ranged from 5.8 to 12.5 h during the three sampling periods (Fig. 22a). Animals from the treatment group spent significantly less time resting during post-calving (*P* = 0.04) and the insect season (*P* = 0.01), whereas there was no difference during late winter (*P* = 0.34) (Fig. 22a). Trends in daily time spent active were the reciprocal of time spent resting. For the control group, daily time active ranged from 11.5 (estimated value) to 18.1 h (Fig. 22b). For the treatment group, daily time spent active was significantly greater during post-calving (*P* = 0.03) and the insect season (*P* = 0.01) (Fig. 22b). A similar trend of greater daily time spent active for overflown animals was apparent during late winter, but the differences in this season were not significant (*P* = 0.15). In the extreme, treatment animals were active for an average of 21 h/day during the insect season.

Daily activity counts for control animals ranged from 3,288 during late winter to 28,179 in the insect season, illustrating substantial seasonal differences in activity. Proportional activity counts (i.e., total counts per day/ total counts per season) for control animals, however, were 0.17 in all seasons (Fig. 23). Animals from the treatment group had higher overall daily levels of activity (i.e., higher proportional activity counts) only during post-calving (*P* = 0.01). The proportional total count for treatment animals during post-calving was 0.21, which translates to an actual count of 35,051. A similar trend of higher counts for treatment animals also was apparent in late winter, but the difference was not significant (*P* = 0.36).

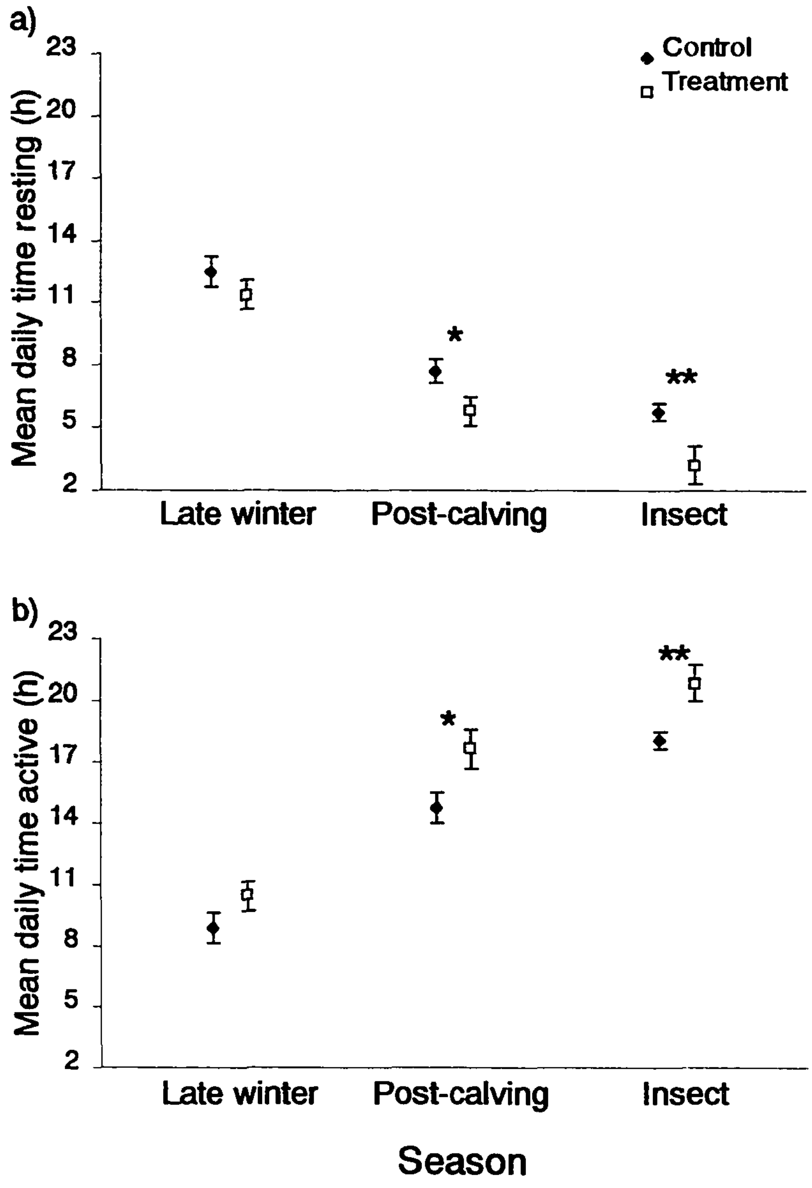

Fig. 22 Comparison (ANOVA) of the total time spent a) resting and b) active for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. Number of asterisks denotes the level of significance (i.e., * = $p \leq 0.05$; ** = $p \leq 0.01$) of differences between control and treatment groups for a particular season.

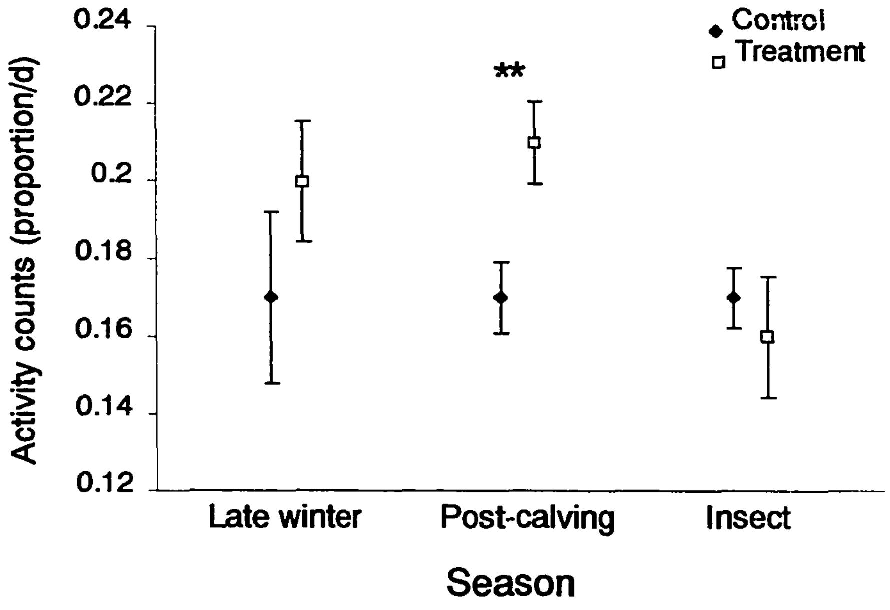

Fig. 23 Comparison (ANOVA) of proportional total counts (i.e., counts per day/total counts per season) for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. Double asterisks denote a significant difference between control and treatment groups ($p \leq 0.01$).

Movements

Distances traveled by animals that were and were not overflown during late winter and the insect season did not differ ($P = 0.48$ and $P = 0.45$, respectively) (Fig. 24). Animals that were overflown during post-calving, however, traveled significantly farther than did animals that had not been overflown ($P = 0.01$).

Regression Models

The amount of variation in resting cycles and movements of treatment animals attributable to specific aspects of noise was evaluated with regression analysis. The 3 noise descriptors used as independent variables all were correlated with one another; the loudest overflight of the day and the average noise level (L_T) were highly correlated ($r = 0.98$) in all seasons and the loudest overflight of the day was highly correlated with number of overflights ≥ 85 dBA and ≤ 1 km per day both during post-calving ($r = 0.70$) and the insect season ($r = 0.79$).

During late winter, all 3 response variables associated with resting were significantly related to noise exposure. Specifically, the number of resting bouts was significantly related to the number of overflights (NF) (number of resting bouts = $3.53 + 0.061\mathrm{NF}$; $r^2 = 0.52$, $F = 5.81$, $P = 0.03$), mean duration of resting bouts was related negatively to number of overflights ($4.37 - 0.130\mathrm{NF}$, $r^2 = 0.50$, $F = 5.63$, $P = 0.03$), and the daily time spent resting was related negatively to the time-averaged noise level (L_T) ($14.0 - 0.032L_T$, $r^2 = 0.46$, $F = 6.98$, $P = 0.04$).

During post-calving, none of the regression models relating resting cycles to noise were statistically significant ($P \geq 0.08$), and the amount of variation explained by all of the models was low. Similarly, none of the models for the insect season were significant ($P \geq 0.12$), although the amount of variation explained by two of the models was approximately 50%.

Regression models relating daily distance moved by treatment animals to various noise variables were not significant ($P \geq 0.51$) during late winter and the insect season; however, a highly significant model ($P = 0.003$) was produced during post-calving.

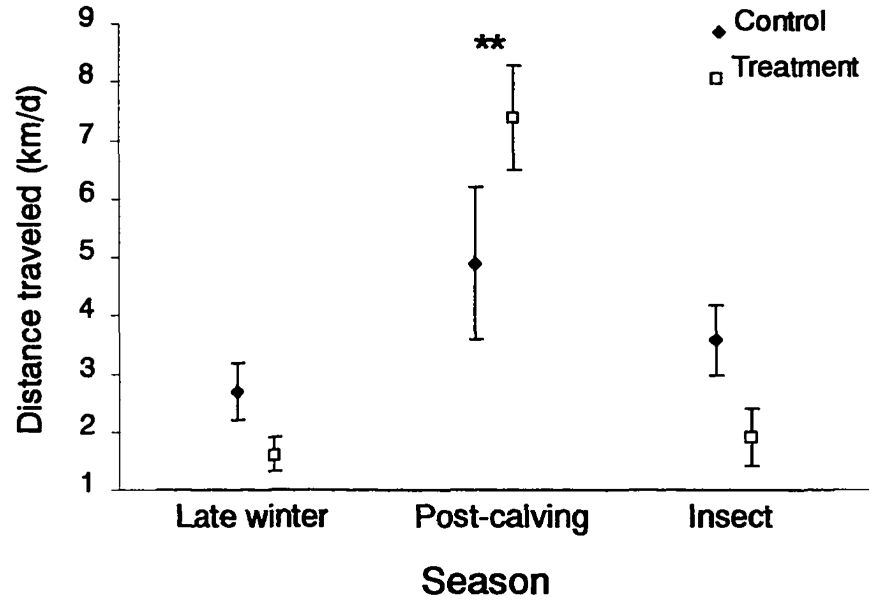

Fig. 24 Comparison (ANOVA) of daily distance traveled (km) for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. Double asterisks denote a significant difference between control and treatment groups ($p \leq 0.01$).

This model selected the loudest overflight of the day (LSEL) as the best variable for accounting for variation in daily distance moved ($r^2 = 0.52$; F = 4.72; $P = 0.003$; n = 32; Distance moved = 1.39 + 0.476LSEL).

Discussion

Two aspects of the behavioral responses of caribou to low-altitude overflights were evaluated: activity cycles and movements. The influence of overflights by jet aircraft on daily activity cycles and movements of caribou was addressed to provide an index to whether the energetics of the animals, as represented by 24-h feeding and resting cycles and movements, were being influenced by these overflights.

Response to disturbance may be acute, chronic, or both. Acute behavioral and heart-rate responses to disturbance generally are short-term in nature (Krausman et al. 1993, Murphy et al. 1993, Weisenberger et al. 1996). Heart rates return to baseline levels within 3 min of the perceived disturbance (Krausman et al. 1993, Weisenberger et al. 1996). Murphy et al. (1993), however, noted significant changes in activity budgets (a longer term measure of response) of disturbed caribou. Caribou spent less time lying and more time either feeding (post-calving) or walking (insect season) in response to low-altitude jet aircraft overflights (Murphy et al. 1993). This increased activity was manifested in long-term (> 10 day), chronic effects on daily movements and activity during the post-calving and insect seasons, respectively.

Activity Cycles

Of the 7 variables related to daily cycles of activity (i.e., number of resting and active bouts, mean duration of resting and active bouts, daily time spent active and resting, and daily activity counts), duration of bouts and daily time spent active and resting were the most useful variables for assessing effects of overflights. These activity variables most accurately reflect the way that caribou balance energy intake with output. Mean duration of resting bouts is influenced primarily by forage quality, independent of forage availability, because lower quality, high-fiber forage requires longer rumination time (Blaxter 1962; Hungate 1975; Van Soest et al. 1988; Russell et al. 1993), that is, as resting bout lengths are shortest when quality is high and availability is low and longest when quality is low and availability is high (Chapter 2). The relation between mean duration of resting bouts and forage availability is exaggerated in extreme conditions (e.g., deep snow conditions) when caribou choose to save energy by increasing lying time rather than search for forage in deep or hard snow (Skogland 1984). Similarly, strong winds result in longer resting bouts in winter (Skogland 1984, Russell et al. 1993). Harassment by insects may result in shorter resting bouts as caribou interrupt resting bouts to move to insect-relief habitat (White et al. 1975, Skogland 1984, Russell et al. 1993) (see also Chapter 2).

Mean duration of active bouts generally is indicative of forage availability within a season because a decrease in availability results in an increase in search time (Russell et al. 1993). Duration of active bouts, however, is negatively related to biomass, between seasons, as energy-maximizing strategies interact with an increase in the rate of food passage (White et al. 1984) to maximize the number of cycles per day (Forchhammer 1995). Forage availability is negatively affected by caribou density (Skogland 1985, 1986, 1990), habitat patchiness (Reimers 1980), and overgrazing (Skogland 1983, 1984, 1990), as well as by snow characteristics, particularly snow depth (Skogland 1984, Russell et al. 1993) and snow hardness (Skogland 1984, Russell et al. 1993). Interactions between forage quality and availability confound the situation further, because active bouts will be of similar length in all instances except when both availability and quality are low, which produces long active bouts (Chapter 2).

Daily time spent resting is an independent measure of the amount of time necessary for digestion of forage, whereas the daily time spent active is indicative of search time necessary to meet the energetic needs of the animal in addition to other activities (Reimers 1980, Chapter 2). Both of these variables integrate the activities for the day -- forage quality, availability, effects of abiotic factors, and predator avoidance. Daily activity counts integrate total activity for the entire day and are useful for comparison among days, particularly in animals with both treatment and control days and for comparisons between seasons. The complex relation between range quality (measured as forage quality and availability) and activity patterns necessitates the use of an experimental design including control and treatment animals.

Based on the activity cycles of undisturbed caribou (i.e., control animals), caribou were least active during late winter, more active during post-calving, and most active during the insect season; daily time spent active for control animals averaged 11.2, 14.8 and 18.1 h, respectively, during these three sampling periods (Fig. 22b). Activity counts collected using a mercury tip-switch are subject to freezing at temperatures of < -32 C (Maier et al. 1996), which could account partially for the lower counts in late winter. Nonetheless, the lower activity counts in winter are most likely due to decreased activity in winter because, although temperatures fell below -30 C during the night, activity counts were still registering which would not occur if the tip-switch were frozen (Maier et al. 1996). Seasonal differences in patterns of activity have been documented for a number of caribou herds in Alaska (Roby 1978; Boertje 1981, 1985; Russell et al. 1993) and basically result from seasonal differences in food resources and environmental variables (e.g., snow depth, insect harassment, predation, photoperiod), the presence of neonatal calves in early summer, and breeding behavior during the rutting season. Additionally, in Chapter 2 we documented between-herd differences and between-season differences in activity patterns of Delta Herd caribou, resulting largely from nutritional constraints. Because of these natural differences in activity among seasons, we evaluated responses to disturbance on a seasonal basis to identify potentially sensitive times of the year.

Although the intensity of responses to low-altitude overflights differed by season, treatment animals exhibited consistent trends of increased activity and decreased resting compared with control animals during all three sampling periods. In late winter, a significant increase in the number of daily resting bouts (Fig. 20a) was associated with a near significant increase in mean active bout duration (Fig. 21b). The trend toward increasing activity by treatment animals was stronger in post-calving caribou and resulted in a significant decrease in daily time spent resting (Fig. 22a) and a 2.8-h increase in daily time spent active (Fig. 22b). Daily activity counts of treatment animals also increased compared with control animals in the post-calving period (Fig. 23). During the insect season, treatment animals had shorter resting bouts (1.4 h) and longer active bouts (3.4 h) than did control animals. Daily time spent active for treatment animals (20.1 h) was at an extreme for all conditions evaluated (Fig. 22b). Thus, although instantaneous behavioral responses to overflights were mild (Murphy et al. 1993), the cumulative effect of overflights was evident in daily cycles of activity.

Movements

Daily movements were evaluated to determine whether treatment animals would respond to overflights by jet aircraft by traveling farther than control animals. Distance traveled did not differ between treatment and control animals during late winter, perhaps because snow can provide significant resistance to movement (Fancy and White 1985, Russell et al. 1993) or because caribou were less responsive to disturbance at this time of year. Milder reactions in late winter also could be associated with calves being nearly 1-yr-old and hence less vulnerable to disturbance than neonatal calves.

In the post-calving period, treatment animals traveled significantly farther than did control animals, and these results indicate that the presence of newborn calves in June may cause female caribou to respond more strongly to disturbance than at other times of the year. This increased movement during post-calving corresponds with the increased activity level discussed previously and suggests that disturbed caribou with young calves are more likely to move in response to disturbance than at other times of the year. This increased locomotion in response to overflights was not detected in analyses of caribou activity budgets (Murphy et al. 1993). There are no data to evaluate whether treatment animals during post-calving were trying to move from the disturbance zone. Dau and Cameron (1986), however, demonstrated that caribou with neonatal calves will avoid areas with disturbing stimuli.

The increased movement observed during post-calving probably was of low energetic cost because the caribou moved only an additional 2.5 km/d, and because the energetic costs of locomotion for caribou are lower than for any other ungulate evaluated to date (Fancy and White 1987). If the caribou moved to less productive habitat, however, there would be additional costs, as was demonstrated for bighorn sheep (Bleich et al. 1990, 1994). In addition, it has been shown that small changes in habitat quality can have multiplicative effects on caribou productivity (White 1983). Changes in distance moved and habitat use also may change the probability of encountering predators. Harrington and Veitch (1992) reported that females exposed to overflights were more likely to lose their calves. Nevertheless, they were not able to determine whether these calves were actually dead or simply separated from the radiocollared mother. If overflights are increasing chances that caribou will encounter predators, or if overflights are increasing the chance of the newborn calves being separated from their mothers, thereby, increasing its vulnerability to starvation and predation, then these potential consequences of aircraft disturbance could lead to population-level effects and should be investigated more thoroughly.

Distance traveled during the insect season also did not differ between treatment and control animals, but activity counts were significantly higher for treatment animals during this season. These results suggest that movements during the insect season were not directional and that the net distance traveled might not accurately describe caribou responses to aircraft disturbance during this season. In addition, insect harassment of caribou causes an increase in daily activity (White et al. 1975, Murphy and Curatolo 1987, Russell et al. 1993) to such an extent that other stressors may not have a detectable effect. Perhaps caribou did, indeed, increase daily movements, but did so within a restricted area rather than moving unidirectionally. Thus, the perceived movement (i.e., the movement that is measured) would be smaller than real movement (i.e., the distance actually traveled) (Laundré et al. 1987). Laundré et al. (1987) reported that perceived movements calculated using daily relocation data were not related to real movements of coyotes (Canis latrans), pronghorn antelope, bobcats (Felis rufus), and mallards (Anas platyrhynchos). They concluded, however, that perceived movements may be validly used to describe long-distance movements such as movements during dispersal. Caribou clearly did not respond to aircraft disturbance in the insect season by leaving the disturbance area, though they did increase their overall activity level.

Regression Models

Models of daily resting cycles from activity counts and daily movements of treatment animals regressed against three measures of noise exposure were developed to evaluate whether any specific aspect of noise was responsible for observed variations in behavior or movements. Resting variables were significantly related to noise variables in late winter with the number of bouts increasing with the number of overflights and the mean duration of resting bouts and daily time spent resting declining with number of overflights and time-averaged noise level, respectively. The most highly significant model was developed for the post-calving season, when the loudest overflight of the day was highly correlated with variation in daily movements.

Seasonal differences in activity and movement patterns were evident for undisturbed caribou indicating that the annual activity cycle of caribou is complex and variable. The responses of caribou to low-altitude overflights by jet aircraft also varied seasonally indicating that these different natural sources of variation must be considered when evaluating anthropogenic sources. During late winter, caribou naturally were moving less because of the high energetic cost of traveling through snow and, accordingly, their response to disturbance did not entail increased movement. Overall, reactions to overflights were mild during this season. During post-calving, caribou were moving more than in any other season, although the difference was not significant when comparisons were made with the insect season. Activity levels during post-calving generally were intermediate between late winter and the insect season. Reactions were strongest during this season. During the insect harassment season, caribou moved less than caribou did during post-calving. Caribou were more active, however, during the insect season than in either the late winter or post-calving seasons. Caribou responses to jet aircraft disturbance were intermediate in this season.

Overall, the results of this study indicate that reactions to overflights were mild, but that modifications of activity cycles and daily movements were evident for caribou exposed to overflights. For the three seasons that were evaluated, severity of responses to overflights was inversely related to age of calves accompanying females under study (i.e., responses were most prevalent when young calves were present). We conclude that females with young are more sensitive to aircraft disturbance. Accordingly, mitigation of military training exercises should be a priority during calving and post-calving.

We also are concerned that aircraft disturbance could have deleterious effects on daily energy balance in years when range quality is low, particularly during the insect season. Summer nutrition is critical for gains in body mass necessary for successful reproduction (Allaye-Chan 1991, Cameron et al. 1993, Cameron 1994, Cameron and Ver Hoef 1994) and survival through winter (Albon et al. 1983, Clutton-Brock et al. 1983). Female caribou subjected to severe insect harassment enter the rutting period in poorer condition and may not achieve the body mass necessary for successful conception (Cameron et al. 1993, Cameron 1994, Cameron and Ver Hoef 1994, Gerhart 1995). Survival of male and female caribou through winter also may be compromised by severe insect harassment. Anthropogenic disturbance by jet aircraft may exacerbate the situation when caribou are energetically stressed. Long-term data on body mass of female caribou of the Delta Herd (Valkenburg 1994) revealed that caribou weights of this herd were at their lowest point recorded, thus, suggesting that they may be vulnerable to the potentially exacerbating effects of human disturbance (Chapter 2).

Results of this study may have been considerably different if we had chosen to work with a herd that had little or no previous exposure to overflights by low-altitude jet aircraft (Valkenburg and Davis 1985). Notwithstanding, we believe using the Delta Herd as study subjects addressed germane questions regarding chronic disturbance in a military operations area that overlaps the range of a herd of ungulates. If the ultimate question is long-term effects of disturbance on a population, then studying the effects of military training exercises on animals that have had an opportunity to habituate best addresses what the nature and extent of long-term effects are likely to be. The finding that this herd had reached a low point in its population growth and individual animal condition

(Valkenburg 1993) also may have contributed to the benign responses exhibited. Delta caribou were likely engaging in a time-minimizing, rather than energy-maximizing grazing strategy, particularly in late winter. Consequently, the results of this study may reflect the response of a nutritionally stressed herd rather than the response of habituated individuals.

CHAPTER 4: ENERGY EXPENDITURES OF CARIBOU RESPONDING TO LOW-ALTITUDE JET AIRCRAFT[4]

Abstract: Anthropogenic disturbance of ungulates has increased in recent decades simultaneously with heightened destruction of habitat and demands for increasing ungulate populations from the consumptive populace. Alaska is in the middle of a controversial expansion of military-training exercises and there is concern regarding the effect these exercises may have on wild populations of ungulates, particularly caribou (Rangifer tarandus) and moose (Alces alces). We investigated the effects of low-altitude overflights by U.S. Air Force (USAF) military jet aircraft on energetics of caribou. Equations relating Wildlink (Wildlink, Inc.) radiocollar activity counts to average daily metabolic rate (ADMR) and incremental energy cost (IEC) of caribou were developed using captive caribou at the Large Animal Research Station, University of Alaska Fairbanks. We evaluated the effects of jet aircraft overflights by U. S. Air Force A-10, F-15, and F-16 jets on energetics of free-ranging caribou of the Delta Caribou Herd in each of 3 seasons: late winter, post-calving, and insect harassment. The noise level experienced by caribou was measured using Animal Noise Monitors (ANMs) that were attached to the Wildlink radiocollars. In late winter, caribou did not respond to overflights by jet aircraft either by increasing IEC of activity or ADMR. Post-calving caribou exhibited a significant, linear increase in both IEC and ADMR in response to the loudest overflight of the day. Insect-harassed caribou did not increase energy expenditure in response to jet aircraft overflights. Caribou were most sensitive to disturbance by military jet aircraft when accompanied by young calves.

Key words: aircraft, caribou, disturbance, energetics, Rangifer tarandus

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[4] Maier, J. A. K., White, R. G., Murphy, S. M., and Maier, H. A. In Prep. Energy expenditure of caribou responding to low-altitude jet aircraft overflights. Can. J. Zool. 00:000-000.

Introduction

Behavioral responses of caribou (Rangifer tarandus) to low-altitude overflights by military jet aircraft include changes in their instantaneous and daily activity (Harrington and Veitch 1991, Murphy et al. 1993, Chapter 3). We hypothesized that these activity responses should be associated with a change in daily energy expenditure. We tested converted activity counts (AC) produced by a mercury tip-switch mounted in a radiocollar (Wildlink, Inc. ® St. Paul, MN, 55444) to incremental energy cost (i.e., energy expenditure expressed as a multiple of energy expenditure of a caribou lying with its head down; IEC). The technique was developed and evaluated with captive caribou and applied to caribou in the wild because ACs could be obtained remotely on a daily basis. This approach is based on converting activity budgets to energy budgets, which previously has been done successfully for wildlife, including caribou (Hudson and White 1985; Fancy and White 1985).

Proposed expansion of training by military jet aircraft in Alaska and Canada is an issue of growing concern. Effects of these training exercises on productivity, primarily of game species such as moose and caribou is unknown (Wadden 1989). Studies have investigated effects of overflights by light aircraft and helicopter on wildlife (Klein 1974, Calef et al. 1976, Krausman and Hervert 1983, Gunn et al. 1985, Valkenburg and Davis 1985, Krausman et al. 1986, Bleich et al. 1990, 1994), but little is known about the effects of overflights by low-altitude jet aircraft (Manci et al. 1988) and whether these could constitute a disturbance (Chapter 3). Response to these concerns, coupled with requirements of the National Environmental Policy Act (NEPA) for military exercise, prompted the USAF to convene a "Research Needs Workshop" in April 1988 on the "Effects of Aircraft Noise and Sonic Booms on Fish and Wildlife" (Asherin and Gladwin 1988). This paper details some of the research conducted in response to these perceived needs.

Determining whether the effects of aircraft overflights results in a disturbance to the productivity of a wildlife species is complicated by the inherently unpredictable behavior of animals and the stochasticity of natural systems. Stochastic events can lead to variation in herd activity, condition, and productivity (Russell et al. 1993, Chapters 1, 2, 3). Thus, it is necessary to measure acute and chronic responses in long-term studies which themselves may have costly chronic effects on the exposed population. A more proximal measure of response, such as energy, can be used to predict likely population changes when its currency is convertible to a population or demographic response. The energy expenditure of individuals and the energy limitations on caribou productivity is well studied (White et al. 1975, Boertje 1985, Fancy 1986, Russell et al. 1993).

Energy expenditure and costs of activity are well documented for caribou (White and Yousef 1978; Fancy and White 1985; Luick and White 1985; White and Fancy 1986). Effects of energy and nutrition on fecundity is known quantitatively (Cameron et al. 1993; Gerhart et al. 1993), and seasonal energy budgets for caribou have been assessed from evolutionary and ecological perspectives (White et al. 1975; Boertje 1981, 1985; White 1983; White and Fancy 1986; Klein et al. 1987; Russell et al. 1993). This knowledge provides a strong framework with which to assess effects of disturbance. The assessment of energy expenditure of wild animals in a field setting is, however, constrained by availability of adequate techniques (White 1993).

Mountainous terrain and the migratory nature of caribou precluded the use of direct observation to determine the daily activity budgets of free-ranging caribou because animals are frequently out of sight. Therefore, we used a remote-sensing technique to obtain the diel pattern of activity counts (Chapters 1, 2, 3). We tested and eliminated heart-rate (HR) monitoring as a technique to estimate energy expenditure of wild caribou (White et al. 1994), although this technique is well suited to captive animals (White and Fancy 1985). Also, we eliminated the doubly-labelled water technique that has been calibrated for caribou (Fancy et al 1986) because it integrated energy expenditure over a number of days (> 10 d), whereas we were interested in daily responses.

One problem in determining if the effects of human-evoked sounds constitute a disturbance on animals in their natural environment is our ability to measure the sound "dose" received by free-ranging animals. We used prototype animal noise monitors (ANMs; BBN Systems and Technologies) to record and quantify the sound levels that caribou were exposed to during low-altitude jet aircraft overflights. Results of this evaluation are reported in the literature (Murphy et al. 1993) and in Chapter 3.

The implications of disturbance on caribou varies depending on the type of disturbance, time of year and the group composition (Gunn et al. 1985; Murphy and Curatolo 1987; Harrington and Veitch 1991, 1992). The goal of this research was to estimate the energy cost of caribou responding to overflights by low-altitude, subsonic jet aircraft. Specifically, we tested the null hypothesis that daily incremental energy costs and average daily metabolic rate would not differ between caribou that had been exposed recently to overflights by jet aircraft and animals that had not been overflown. Caribou from the Delta Herd in interior Alaska were selected for study because this herd occurs near Eielson Air Force Base in interior Alaska. Three field periods, typifying major seasons in caribou life history, were chosen for study; namely, late winter (March-April 1991), post-calving (June 1991) and the insect-harassment season (July-August 1991). Our specific objectives were to: (1) determine incremental energy costs from daily activity budgets of captive caribou; (2) correlate incremental energy cost with simultaneously determined activity counts of captive caribou; (3) determine daily incremental energy cost and average daily metabolic rate of wild caribou; and (4) correlate daily incremental energy cost and average daily metabolic rate with sound dose to estimate the energy cost of responding to low-altitude jet aircraft overflights.

Methods

Technique development with Captive Animal Studies

Estimation of heart-rate: We assumed that if activity counts can be used to estimate energy expenditure, then temporal changes in activity counts should closely correlate with recognized quantitative indices, such as heart-rate (Fancy and White 1985, White and Fancy 1985) and observed activity budgets (Boertje 1985, Fancy and White 1985, White 1993). Heart-rate (HR) was used to further calibrate Wildlink activity counts (AC) as a measure of energy expenditure. Three caribou held at the Large Animal Research Station (LARS), Institute of Arctic Biology, University of Alaska

Fairbanks were fitted with HR transmitters implanted subcutaneously (Fancy and White 1986). For this system, each heart beat is detected and transmitted, a datalogger records the transmission, and sums the number of beats every minute. This system was evaluated for signal distortion and reliability while animals were engaged in typical activities (e.g., walking, standing).

Estimation of activity counts: The Wildlink activity-monitoring system is composed of a mercury tip-switch and a computer chip that registers a count (i.e., activity count) each time the collar is tilted. The ACs, accumulated during 36 equal-length intervals (ranging in length from 1 to 90 min), are retrieved remotely using a triggering transmitter that signals the collar to respond by transmitting data in binary code (Maier et al. 1996). Data are received using a standard Telonics receiver (Telonics, Inc. ® Mesa, AZ, 85204), recorded by hand, and later translated to Arabic numerals in the appropriate time interval (Mech et al. 1990, Kunkel et al. 1991).

Estimate of activity budgets: Behavioral observations were conducted on 3 captive adult (≥ 2 y) male caribou and 3 adult female caribou and their calves at LARS once monthly for 26 h using focal-animal, all-occurrence sampling (Altmann 1974). Caribou were housed in pens ranging from 0.1 to 3 ha. Recorded behaviors included: lying; standing; feeding; grazing; drinking; cratering; rubbing antlers; sparring; walking; running; playing; and nursing. Observers watched caribou from towers and entered behaviors into a laptop computer using a program (DIAP) developed at LARS for this purpose. Initial behaviors were entered for all focal animals at the onset of each observation period; thereafter, new entries were made as the animal entered new activities.

Estimate of Incremental Energy Cost and Average Daily Metabolic Rate: Caribou behaviors were translated to costs of activity relative to lying, that is, the incremental energy cost (IEC), as determined by Fancy and White (1985) (Table 6). The relative cost of each activity (e.g., 1.24 for standing) was multiplied by the time spent in that activity. We summed these values over 30- and 60-min intervals to give estimates of IEC_{30} and IEC_{60}, respectively. Mean IEC for 24h (IEC_{24}) was estimated as the sum of $IEC_{60}/24$. IECs and ACs were plotted over time to determine their relation.

Average Daily Metabolic Rate (ADMR) ($kJ/kg^{0.75}$) of each caribou was estimated as;

$ADMR = IEC_{24} * RMR$,

where RMR is the seasonally adjusted daily resting metabolic rate measured for a fully fed captive caribou while standing (Fancy 1986; 717.8 ± 23.2 (late winter), 942.0 ± 26.6 (post-calving), 990.4 ± 13.4 (insect season)).

Association of HR and IEC with AC:

HR and ACs were measured over 26-h on 3 separate occasions for 3 caribou fitted with Wildlink collars. The diel pattern of HR, IEC, and AC in 10-, 30-, and 60-min time intervals was assessed visually and by regression analysis.

The statistical fit of IEC_{60} to AC_{60} was made using simple linear regression (Kitchens et al. 1993). Equations were developed for each caribou in each observation period. Analysis of covariance was used to test for effects of animal and observation period on regression coefficients (Zar 1984). Equality of Y-intercepts were tested when slopes were homogeneous. To account for between-animal differences in ACs, the leverage test for influential points (Neter et al. 1990) was used and corrections made to these data when necessary. Outliers were removed only when they had more than 2.5 times the leverage of an average point. When both slopes and elevations were homogeneous, data were pooled and an overall equation was developed.

Energy Costs and Metabolism of Overflown Caribou

Field observations were made during late winter (March-April 1991), post-calving (June 1991), and insect harassment (July-August 1991) seasons. The distribution

Table 6. Incremental costs of activities relative to resting metabolic rate from Fancy and White (1985).

Behavior	Incremental cost
Lying-head down	1.00
Lying-head up	1.07
Standing	1.24
Feeding	1.44
Walking	1.81
Running	1.93

of the Delta Caribou Herd (DCH) within its 9,600-km^2 range (Davis et al. 1985) was determined by flying recconnaissance surveys the week prior to each sampling period. Locations of the study areas differed among sampling periods, but were always on the north side of the central Alaska Range (64°14' N, 148°34' W; 63°35' N, 146°14' W).

A treatment and a control group, each composed of 5 adult female caribou, were captured by darting from a helicopter (capture protocol is discussed in detail in Chapter 3). Caribou in the treatment group were scheduled to be overflown by military jet aircraft flying approximately 33 m above the ground. Caribou of the control group were located in areas avoided by jet aircraft ($\geq$ 16 km from the treatment group). We outfitted caribou of each group with Wildlink radiocollars.

Aircraft noise monitoring: Caribou of the treatment group also were outfitted with prototype Animal Noise Monitors (ANMs) that recorded and stored all noise events above an exposure of 85 dBA. Data recorded included sound equivalent level (SEL) and the time of the event. A detailed description of the ANMs and the procedure followed to mount the ANMs on the Wildlink collars is described in Chapter 3. SEL is a measure of the total amount of acoustical energy generated during an event calculated by logarithmically integrating the magnitude of the noise over the time period of the event (American National Standards Institute 1990). For each aircraft overflight, the SEL measured by the ANMs was used to describe the noise exposure experienced by the individual collared caribou or groups of caribou that contained instrumented animals. When ANMs malfunctioned, it was necessary to estimate SEL. Variables required for the estimation of SEL included: aircraft type; number of aircraft; flight speed; power setting; and slant range (i.e., linear distance) from the aircraft to the caribou. USAF pilots provided the air controller with flight speed, power setting, and altitude. Slant ranges were based on aircraft location and on telemetry locations of the animals or on direct observations in the case of observed caribou. Caribou and estimated aircraft locations were plotted on 1:63,000 topographic maps. Slant ranges were calculated using the ATLAS GIS program.

To estimate daily noise exposure for each animal, a time-averaged sound level (L_T) was calculated using the following formula:

$$L_T = 10\log_{10}\left[\frac{1}{T}\sum_{i=1}^{N}10^{SEL_i/10}\right]$$

where SEL_i is the Sound Exposure Level of the ith event in a series of N events over the time period T (American National Standards Institute 1990). Sound measurements used for analyses for each experimental animal, therefore, were daily L_T, the number of overflights greater than 85 dBA (NF), and the loudest overflight of the day (LSEL), and were used as independent variables in regression analyses.

The field crew for data collection included 3 biologists, an acoustician, a Ground Forward Air Controller, a fixed-wing pilot, a helicopter pilot, and a biologist downloading activity data and recording animal locations. The 3 biologists collecting data on activity budgets from direct observations provided a checks-and-balances system for the Wildlink radiocollars. Once on site, the air controller set up radio equipment and established radio contact with USAF A-10, F-15, and F-16 pilots. The air controller notified the pilots of our location and directed the jets along flight paths as requested by the biologists. In most instances, the pilots were directed to fly directly over the treatment caribou at 33 m above the ground at high or full power setting. Multiple overflights were separated by at least 5 min.

One biologist worked closely with the air controller (e.g., requesting specific flight paths and recording flight data relayed from the pilots) and was responsible for precisely mapping the locations of caribou and the path of jets for each overflight. The 2 other biologists collected focal- and scan-animal behavioral data. The acoustician recorded data on weather, flight characteristics, and tended noise monitoring equipment. The helicopter pilot stood by to move the team if necessary.

Noise exposure: The ANMs were used to measure the noise level experienced by caribou at the time of jet aircraft overflights. The prototype ANMs were developed specifically for this project and represent the first time that a measurement of noise exposure was made on free-ranging animals in their natural environment. Prototypes were tested on captive caribou under simulated field conditions at LARS. These tests allowed rapid detection of faults and modification with minimal costs. The ANMs were capable of collecting multiple-sound exposures over long periods of time (in our instance, up to 10 days) under a variety of environmental conditions. Longevity of the ANM is attained by maintaining the device in a semi-dormant state until a series of programmable, predetermined noise thresholds have been exceeded. Thus, only events associated with aircraft overflights were measured and battery life was optimized. The ANMs were pre-programmed to a noise event threshold of 85 dBA, which had to be exceeded for more than two seconds to guard against measuring wind noise. Therefore, an overflight is defined as any exposure to one or more low-flying jet aircraft that exceeded 85 dBA. Once the ANMs were deployed on the caribou they were no longer accessible until retrieval at the end of the study period.

Daily activity was determined using the mercury tip-switch and the energy expenditure was estimated from the equations developed on captive caribou as described above. During each study season IEC_{60} for each collared caribou was estimated from the relation of AC_{60} versus time, as detailed by Murphy et al. (1993) and in Chapter 3 and the seasonally appropriate relationship between IEC_{60} and AC_{60} as derived from captive studies. Data were available for both control and treatment caribou. ADMR of each caribou for each day of the study was estimated using the equation described above. Female caribou were assumed to be pregnant in late winter, and lactating in the post-calving and insect seasons.

We wanted to determine which noise variables, if any, were important in explaining the variation in IEC_{24} and ADMR. Noise variables considered were: (1) number of overflights $\geq$ 85 dBA (NF); (2) loudest overflight each day (LSEL); and

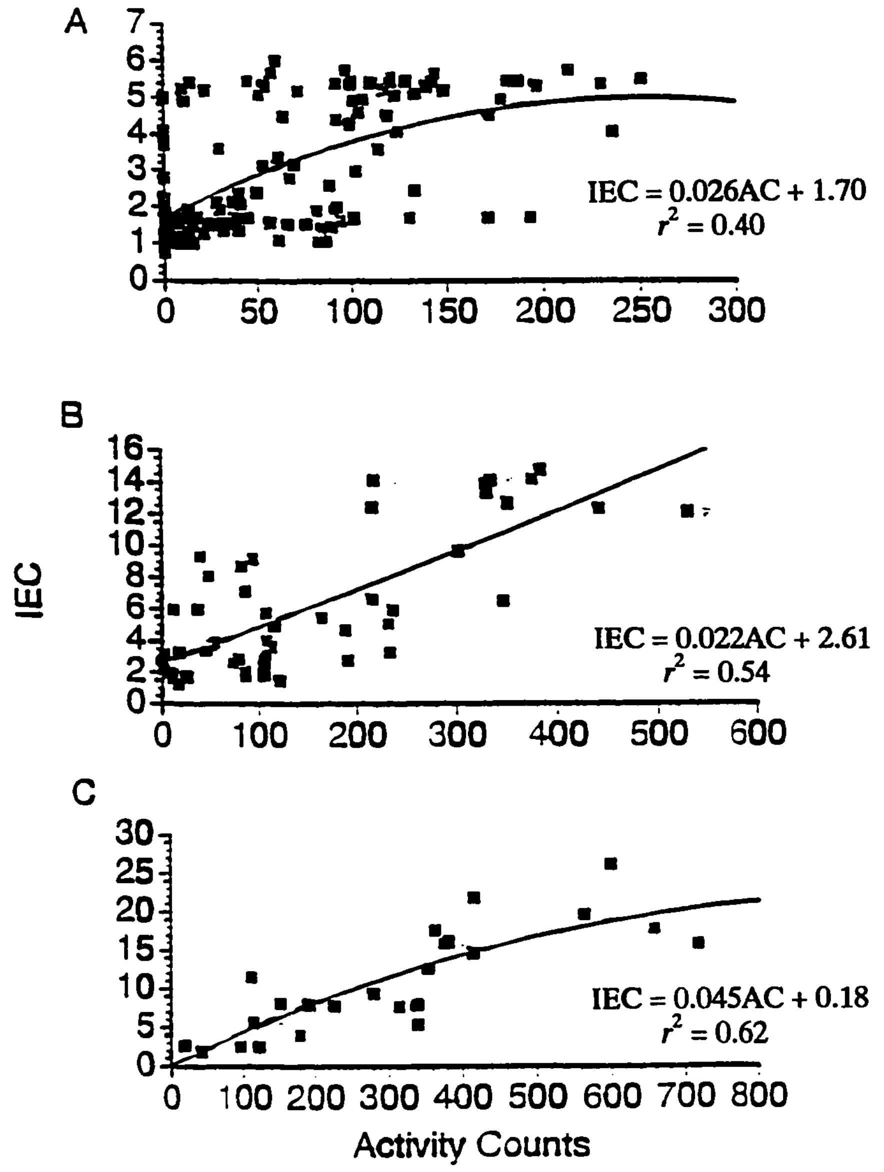

Fig. 25 As interval length increases, predictive capability of IEC from AC improves for captive caribou of the Large Animal Research Station in Alaska. a) 10-min, b) 30-min, and c) 60-min interval length using data from 17 Jul 1991.

(3) time-averaged sound exposure for the treatment day (L_T). We used simple linear regression (SAS) developed using data from animals subjected to low-altitude overflights by jet aircraft in the field. Significance was assessed at $P < 0.10$ level because of small sample sizes.

Results

Captive Animal Studies

Although subcutaneous and externally mounted HR systems can be used to document HR of caribou, the systems we tested suffered from defects that resulted in our rejection of their use for field studies with wild caribou. Implanted Stuart transmitters were rejected because of their propensity to migrate beneath the skin or wear through the skin, resulting in loss of the signal, often within 2-3 weeks of implantation. The problem of transmitter loss may be rectified by sewing the transmitter to the skin with a button on the skin's exterior surface. This procedure, however, was not 100% effective. Reception range at ≤ 1.6 km was a serious limitation and the signal was lost when the animal moved behind a hill. In addition, the signal became weak when the receiver was on the opposite side of the implant. Reception from implanted transmitters at close range was excellent with little distortion due to animal movement. For some implants, signals from the transmitter failed completely when the animal was lying. Further, some transmitters worked well on caribou while others did not, either because of individual variation in the transmitter or in the caribou. We conclude that, in the present form, the Stuart Enterprises implantable HR transmitter is limited to use in controlled studies using captive animals or in field studies on comparatively sedentary species. The HR system was rejected for use on wild caribou, however, it was used to confirm patterns in IECs and daily energy expenditure patterns of captive animals. When evaluating the use of HR, we primarily were interested in the relation between HR, caribou behavior, and ACs.

Continuous monitoring of HR was possible in only 3 observation periods due to problems with transmitter loss through the skin and poor reception in the field. A cyclical pattern of HR through 24-h observation period was noted, with HR varying from

35 beats/min while lying with head-down to 220 beats/min when animals were very active (Fig. 26). We estimated IEC predicted from daily activity budget using the coefficients in Table 6. Measures of IEC, HR, and Wildlink ACs were synchronously related (Fig. 27).

Models produced using simple linear regression indicate that a long time interval (e.g., 60-min) results in a higher amount of variation in IEC accounted for by the independent variable AC ($r^2 \geq 0.78$; Table 7) than seen in models produced using a shorter intervals of time (i.e., 10- or 30-min; $r^2 = \geq 0.62, \geq 0.72$, respectively). Good concordance was noted in comparisons of HR, ACs and IEC over intervals of 30- and 60-min (Fig. 28). For both intervals, lying and active periods were clearly detectable, however, the 30-min interval yielded no extra information over 60-min. The variables have different magnitudes when summed over 60 minutes, but track each other closely.

A comparison of relations of hourly HR and ACs with IEC summed over 60-min showed highly significant relations between IEC and AC (Table 7). In all 3 studies AC60 was more highly correlated with IEC60 than was HR. Likewise in these studies on HR60 (beats/h) was highly correlated with AC_{60}. HR_{60} intercepts did not appear to change with season and represent the same range of HRs, 39-41 beats/min, measured in caribou at rest in December and January (Fancy 1986). Slopes of the regression lines were significantly different ($P > 0.002$) between dates. Close concordance between HR and ACs support the use of ACs also (Table 8). Therefore, a set of empirical relations between IEC_{60} and AC_{60} was constructed through 6 months of the year at LARS (Table 9). Female and male caribou were used and relations were assessed by covariance analysis for to determine if animals and months were different or whether data could be combined. The equation for female caribou F3 in March was used to predict IEC_{60}s during the late winter studies of caribou of the Delta herd. Likewise, F3's equation for July (Table 9) was used to predict IEC_{60}s for wild caribou during the post-calving and insect seasons.

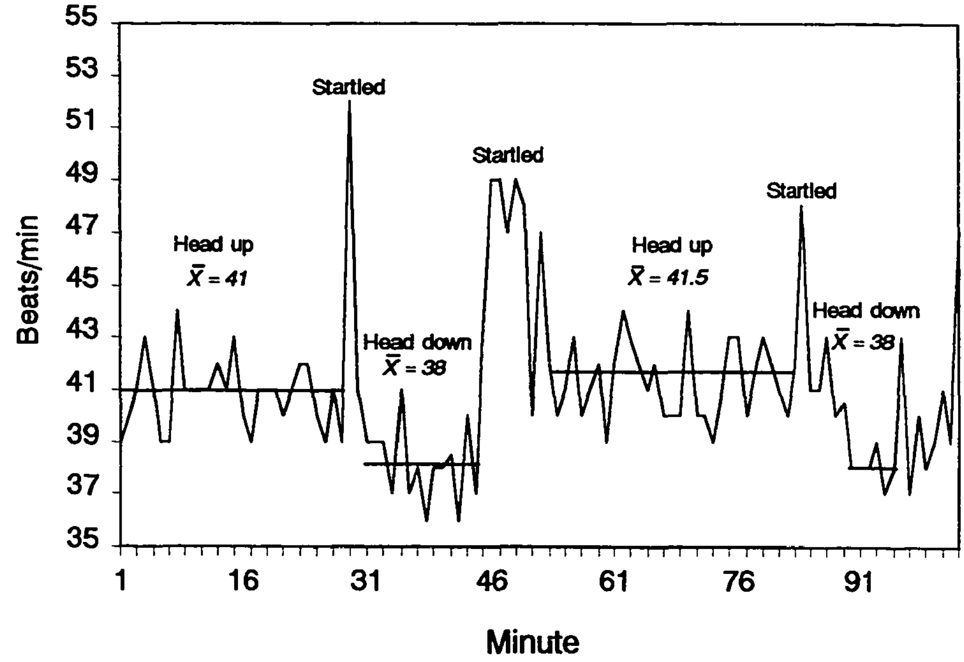

Fig. 26 Typical heart-rate (HR; beats/min) in relation to time (min) of a caribou while lying with head down on the ground or head up. Also shown are HR excursions due to startling by other caribou and activity of humans. HR was recorded by a subcutaneously implanted Stuart HR transmitter while the animal was resting in a small pasture at the LARS, Alaska. Data were collected in April 1991.

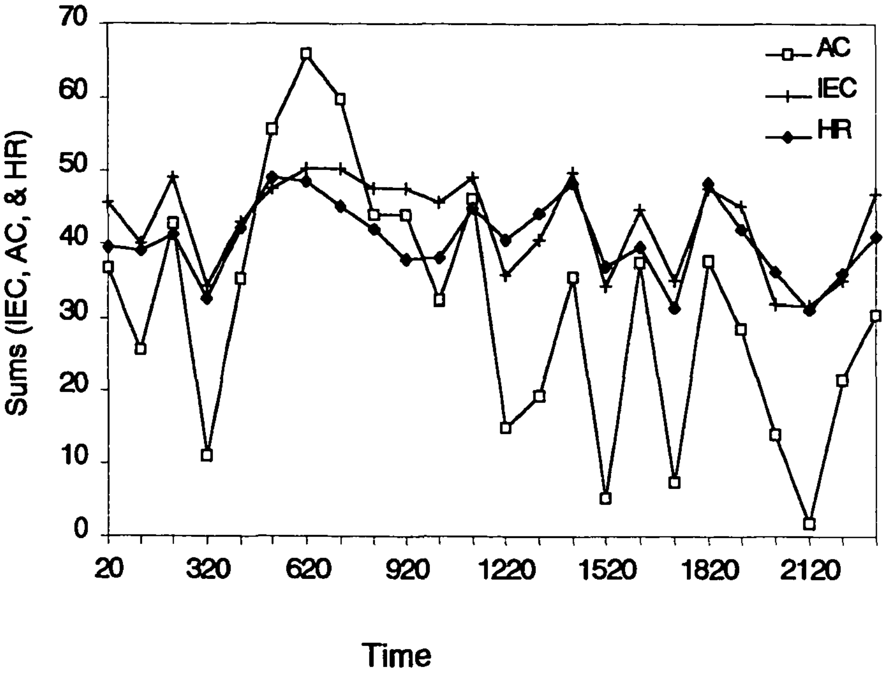

Fig. 27 Typical diel pattern of heart-rate (HR; beats/min) in relation to incremental energy cost (IEC; based upon the daily activity budget and calculated using incremental energy costs of behavior (Fancy and White 1985)) and activity counts (AC) from the Wildlink collar. The adult (≥ 2 yr) male caribou was grazing a small pasture at the LARS, Alaska; 16 Jan 1991.

Table 7. Comparison of relations between hourly incremental energy cost (IEC) from heart-rate (HR) and activity counts (AC). Data were collected on captive caribou at LARS in Alaska.

Date	Model	N	r	SE	*P*
9 Dec 1990	IEC = -0.46 + 0.0006HR	26	0.781	0.145	<0.0001
	IEC = 1.06 + 0.0005AC	26	0.965	0.062	<0.0001
16 Jan 1991	IEC = 0.13 + 0.0004HR	26	0.818	0.126	<0.0001
	IEC = 1.03 + 0.0005AC	26	0.938	0.080	<0.0001
30 Jan 1991	IEC = 0.20 + 0.0004HR	26	0.818	0.118	0.0001
	IEC = 1.03 + 0.0006AC	26	0.860	0.113	0.0001

N, No. of observations; r, correlation coefficient; SE, standard error of the estimate; *P*, levels of significance of r.

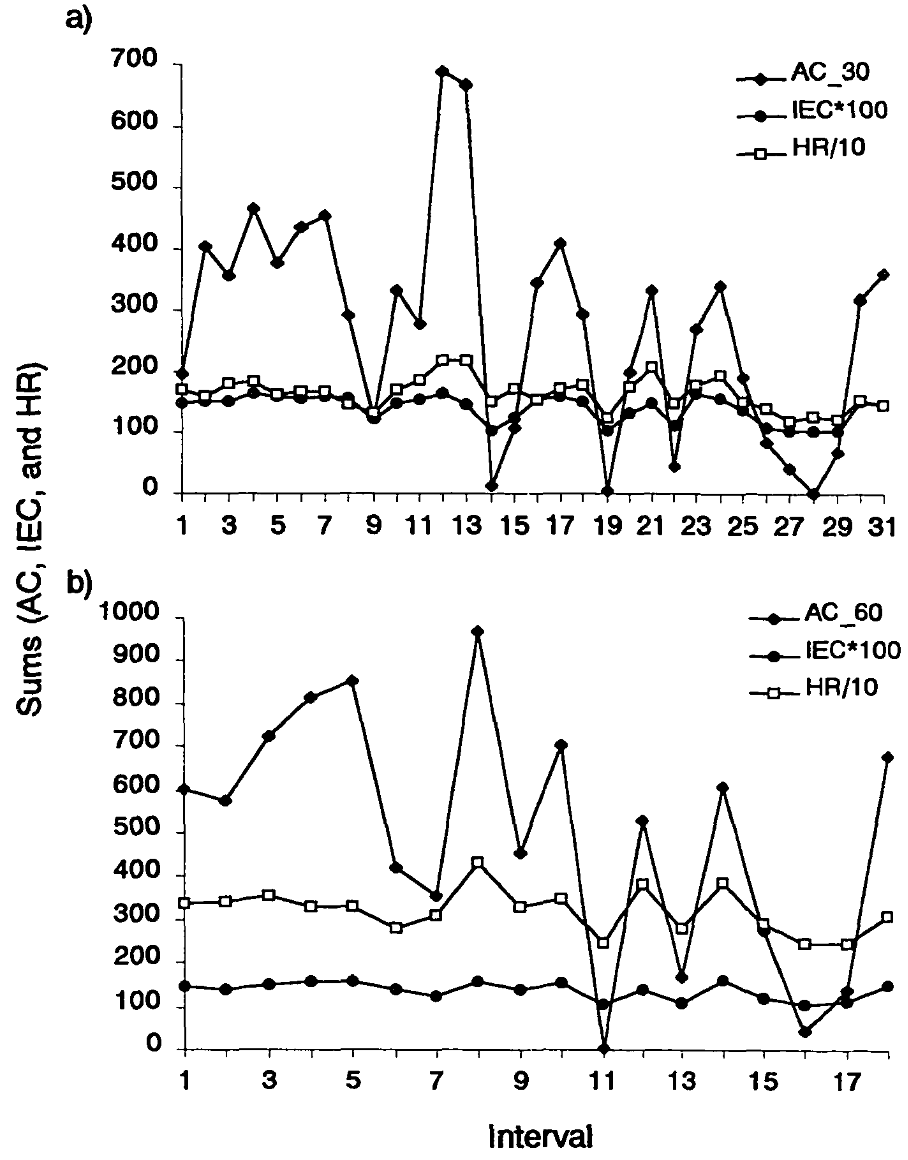

Fig. 28 Comparison of AC with HR and IEC when analyzed on a 30- (a) or 60- (b) min time interval. The caribou was fitted with a Wildlink activity sensor and an implanted HR transmitter and was observed continuously to construct an activity budget. The activity budget was converted to an incremental energy cost (IEC) using coefficients in Table 6. The caribou was grazing in a large pasture at LARS, Alaska; 17 April 1991.

Table 8. Correlation of heart-rate (HR_{60}; beats/h) with hourly activity counts (AC_{60}). Data were for a male caribou grazing a small pasture at the LARS, Alaska. HR_{60} data were recorded from an implanted HR transmitter and AC was obtained from a Wildlink collar.

Date	Model	r	SE	*P*
9 Dec 1990	$HR_{60} = 2919 + 0.48AC_{60}$	0.662	232	0.002
16 Jan 1991	$HR_{60} = 2332 + 0.81AC_{60}$	0.873	203	<0.001
30 Jan 1991	$HR_{60} = 2477 + 1.49AC_{60}$	0.832	290	<0.001

r, correlation coefficient; SE, standard error of the estimate; *P*, level of significance of r.

Table 9. Regression of hourly incremental energy cost (IEC_{60}) on Wildlink activity counts (AC). IEC_{60} was estimated from activity budgets of tame caribou grazing as mixed sex groups in a large pasture at the Large Animal Research Station, Alaska. Data were collected monthly (1991 - 1993).

Animal	β_o	β_1	r	SE
December				
M3	1.06	0.0005	0.969	0.062
January				
M2	1.02	0.0008	0.824	0.092
M3	1.03	0.0006	0.860	0.113
February				
M1	1.03	0.0008	0.943	0.059
M2	1.02	0.0007	0.806	0.109
M3	1.05	0.0008	0.866	0.090
March				
M2	1.05	0.0003	0.700	0.118
F1	1.10	0.0003	0.824	0.075
*F3	1.21	0.0002	0.894	0.100
July				
M1	1.00	0.0005	0.831	0.060
F1	1.02	0.0001	0.911	0.050
F2	1.03	0.0002	0.640	0.091
*F3	1.05	0.0002	0.889	0.056
September				
M1	1.05	0.0010	0.900	0.070

* Equation used to predict IEC for wild caribou.

Energy Costs and Metabolism of Overflown Caribou

Relations of Wildlink ACs to IEC using captive caribou were used to test whether wild caribou altered their energy budgets in response to overflights by jet aircraft. IEC_{24} for animals in the control groups ranged from 1.24 to 1.29 during the three sampling periods (Fig. 29a). Although IEC_{24} was higher by 1-3% in 2 of 3 instances for the treatment animals, only the increase in post-calving was significant ($P \leq 0.10$). In control animals, IEC_{24} was similar for each season with highest values occurring in the insect season.

ADMR for control and treatment days were not significantly different in late winter and insect season, but ADMR on treatment days exceeded controls during post-calving ($P \leq 0.10$, Fig. 29b). In late winter, average daily metabolic rate of control animals was lower than subsequent seasons ($P = 0.0001$), whereas estimates for post-calving and the insect season were almost identical ($P = 0.65$).

Influence of the "dose" of sound, as given by the following variables, number of overflights $\geq$ 85 dBA (NF), loudest overflight each day (LSEL) and time-averaged sound exposure for the treatment day (L_T) was minimal for late winter and the insect season. LSEL consistently was the sound variable with highest predictive power (Table 10). For post-calving females, both IEC_{24} and ADMR increased significantly ($P \leq 0.05$) in response to LSEL (Table 10).

One of the difficulties associated with outdoor noise measurement is background environment noise, particularly wind. Even moderate winds caused the ANMs to record so the ANMs were programmed to a threshold level of ≥ 85 dBA. There were several technical problems with the prototype ANMs. In late winter, the cold weather (-32° C at night) caused the ANMs to discharge on several occasions resulting in battery failure in 2 of 5 units. Unit reliability was variable such that some units were consistently reliable and others consistently had problems in all sampling periods (Murphy et al. 1994).

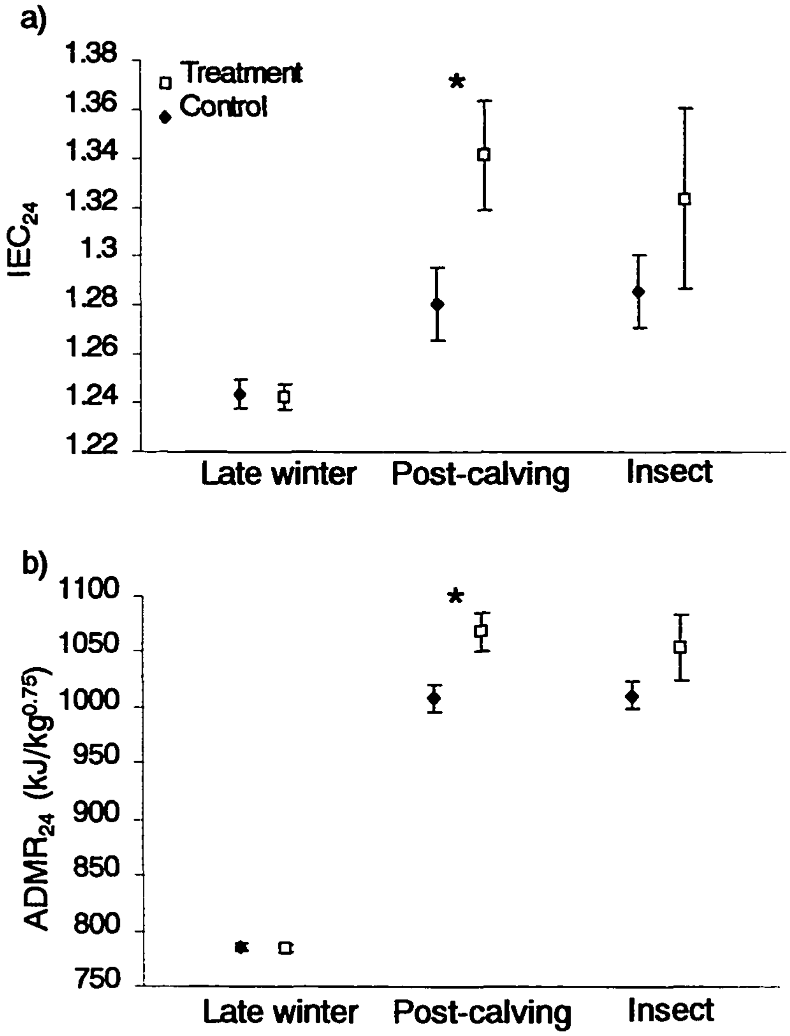

Fig. 29 Comparisons (ANOVA) of energy expenditure represented by a) IEC and b) ADMR (kJ/kg$^{0.75}$) for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. An asterisk denotes a significant difference between control and treatment groups ($p \leq 0.05$).

Discussion

Measuring energy responses to disturbance using HR is a well documented technique (MacArthur et al. 1979, MacArthur et al. 1982, Geist et al. 1985, Renecker and Hudson 1985, Harlow et al. 1987, Chabot 1993, Krausman et al. 1993, Weisenberger et al. 1996). HR, purportedly, can give an indication of the instantaneous reaction of an animal to a disturbance as well as a measure of the chronic effect if HR is elevated for extended periods. In caribou, there was an increase in HR with change in animal position (i.e., from head down to head up) as seen in elk (Chabot 1993) of 3 to 5 beats/min, equivalent to an O_2 consumption of 48-100 ml/min, (i.e., a 10% increase in resting metabolism; Fancy and White 1985). Floyd (1987) showed that an average startle response is associated with an oxygen consumption of 1-5 ml, equivalent to a caribou moving 1 to 3 m (horizontal distance). This slight change in head position is a common response when an animal becomes alert following an overflight (Murphy et al. 1993).

The mountainous terrain in our study area along with the vast daily distances traveled by caribou, made the use of HR impossible. Our results show a close relation between HR and Wildlink ACs ($P \leq 0.002$; Table 8). This relation allows us to use AC, a remote-sensing technique, in lieu of HR while maintaining good precision. We tested the possibility that Wildlink ACs could be used to estimate hourly and daily energy expenditure of caribou. Calibration of AC with energy expenditure was dependent on a robust time interval for comparison of AC with IEC. Because IEC also is correlated with HR (Fancy and White 1985) data on concordance and correlation of HR with IEC support a strong basis for extrapolation of ACs to IEC under field conditions. When all data sets were analyzed, 60-min was preferred because estimation of daily energy expenditure was more accurate and data acquisition (i.e., collection of 36 units in binary code) was more easily handled. Wildlink AC also enabled simultaneous collection of data on multiple animals and documentation of 24-h group synchrony of activity in caribou and the lack of between-group synchrony in caribou (Chapter 1).

Using remote-sensing resulted in the loss of the high resolution data of the instantaneous reaction to jet overflights but this reaction was shown to be slight and of

Table 10. Linear regression models evaluating relationships between daily incremental energy cost (IEC_{24}) and average daily metabolic rate (ADMR, $kJ/kg^{0.75}$) of caribou and the loudest sound exposure of the day (LSEL) resulting from overflights by low-altitude jet aircraft in Alaska, 1991.

Season	Dependent Equation	Model	r	F	*P*
Late Winter					
(n = 24)	IEC_{24}	1.26 - 0.0002LSEL	0.173	0.57	0.46
	ADMR	797 - 0.119LSEL	0.173	0.61	0.45
Post-calving					
(n = 32)	IEC_{24}	1.14 + 0.002LSEL	0.374	5.17	0.03
	ADMR	897 + 1.52LSEL	0.374	5.08	0.03
Insect					
(n = 11)	IEC_{24}	1.30 + 0.0002LSEL	0.141	0.17	0.69
	ADMR	1023 + 0.156LSEL	0.173	0.24	0.64

r, correlation coefficient; P, significance of r.

short duration in bighorn sheep, desert mule deer (Krausman et al. 1993, Weisenberger et al. 1996), and caribou (Murphy et al. 1993) and may not be a critical issue. Alternatively, long-term changes resulting from disturbance such as changes in habitat use (Bleich et al. 1990, 1994), decreased calf survival (Harrington and Veitch 1992), and increased movement (Bleich et al. 1990, 1994; Murphy et al. 1993; Chapter 3) may be critical issues and are measurable using remote-sensing techniques. Further, Wildlink ACs also are closely related to the IEC and ADMR of caribou ($P < 0.0001$), which enabled us to determine energetic costs of caribou responding to jet aircraft overflights.

Based on AC of undisturbed (control) caribou, it was clear that caribou were less active and had a lower ADMR in late winter than in either post-calving or the insect season; ADMR ($kJ/kg^{0.75}$) for control animals averaged 786, 1012, and 1009 respectively, during these 3 sampling periods (Fig. 29b). Seasonal differences in activity have been well documented for caribou (Russell et al. 1993), although the computer-simulation model (CARIBOU) produced using Russell's data predicted a much higher ADMR for caribou in late winter than was predicted by our study. ADMR values predicted by the CARIBOU model (White et al., in prep) agreed closely with our values in post-calving and the insect season. The differences between CARIBOU estimates and our estimates of ADMR in late winter may be because of the record snow depth experienced by caribou of the Delta herd in winter 1991. Seasonal changes in activity patterns and, thus, ADMR result from seasonal differences in environmental conditions (e.g., snow depth, insect activity) and from physiological adaptations of the animals themselves (e.g., decreased appetite, lowered resting metabolic rate). Because of these natural seasonal differences, it was important to evaluate responses to disturbance on a seasonal basis to identify potentially sensitive times of the year.

In late winter, caribou did not exhibit changes in IEC of activities ($P = 0.73$) or in ADMR ($P = 0.59$) in response to overflights by low-altitude jet aircraft. Nonetheless, in post-calving caribou, there was a significant linear increase in both IEC ($P = 0.04$) and ADMR ($P = 0.04$) in treatment caribou. There also was no associated increase in IEC ($P = 0.40$) and ADMR ($P = 0.39$) in caribou overflown by jets during the insect harassment season. Murphy et al. (1993) reported similar results in short-term (15-min) activity budgets such that there were no significant changes in activity budgets in caribou exposed to overflights in late winter. Post-calving caribou interrupted lying bouts in favor of feeding when subjected to overflights and insect-harassed caribou spent less time lying and more time standing.

The DCH has been described as "the most highly disturbed herd in Alaska" (Davis et al. 1985: pg. 5). These animals have certainly had the opportunity to habituate to many types of disturbance, including low-altitude overflights by jet aircraft. The range of the DCH is within the training zone of USAF A-10, F-15, and F-16 jets out of Eielson A. F. B., Alaska. The calving grounds of the DCH also borders the bombing range used by these jets. Ideally, research regarding the effects of anthropogenic disturbance is conducted in long-term studies using previously undisturbed animals, thus, delimiting the entire range of responses and habituation of animals to anthropogenic events. In the absence of long-term funding, however, studying a herd that may be habituated to the disturbance under question best addresses the question of long-term effects of chronic disturbance of that sort. Although Harrington and Veitch (1992) reported that calf survival was compromised by the frequency of overflights by low-altitude jet aircraft during and immediately after calving in barren-ground caribou, Davis et al. (1985) concluded disturbance of the DCH by military aircraft and other factors did not adversely affect productivity. Davis et al. (1985), however, based their conclusions on annual trends in productivity of the DCH, compared with other herds in Alaska that were not exposed to low-altitude overflights by military aircraft. No direct evaluation of the effects of overflights on individuals was made. Additionally, Davis et al. (1985) did not consider differences in forage quality, forage availability, predation, and weather among herds. Since 1989 there has been a decline in population size of the DCH (Valkenburg 1993) and growth rate of individuals (Chapter 2). We showed, using caribou activity budgets, that the DCH was subjected to poor foraging conditions, particularly in the late winter and post-calving periods (Chapter 2). These results indicate that a reevaluation of the effect of overflights should be made concomitant with an evaluation of the underlying reason for this decline. Our study showed an increase in energy expenditure in response to disturbance by military aircraft in post-calving caribou. Whether this significant increase in energy expenditure of post-calving caribou can lead to an overall decrease in herd productivity is unknown.

Conclusions

Jet overflights in late winter were associated with no change in the IEC and ADMR. Post-calving caribou exhibited a significant, linear increase in both IEC and ADMR with maximum daily sound exposure. In the insect season, caribou appear to expend no extra energy in response to low-flying jet aircraft. It has been shown that female caribou are more sensitive to disturbance events when they are accompanied by young calves (Roby 1978, Cameron et al. 1979, Smith and Cameron 1983). Indeed, the intensity of the response to aircraft overflights is inversely related to calf age. Based on our results we conclude that, though population-level impacts of low-altitude jet aircraft overflights may be minimal, a policy of avoidance during and immediately following calving is recommended. Further research using improved remote-sensing techniques and computer simulation modeling is necessary if we are to better understand implications of anthropogenic disturbance on herd productivity. Such efforts are currently underway (White et al., in prep).

SYNOPSIS

Effects of aircraft overflights on ungulates have focused on short-term behavioral responses (Krausman et al. 1993, Murphy et al. 1993, Weisenberger et al. 1996) or responses have been inferred from indirect measures such as heart-rate (MacArthur et al. 1979, 1982; Krausman and Hervert 1983; Krausman et al. 1993; Weisenberger et al. 1996). Besides being indicative of activity, heart-rate is a correlate of instantaneous energy expenditure (Fancy 1986). Responses of heart-rate to aircraft overflights have been documented for mountain sheep (MacArthur et al. 1979, 1982; Krausman and Hervert 1983; Krausman et al. 1993; Weisenberger et al. 1996) and desert mule deer (Krausman et al. 1993, Weisenberger et al. 1996), and show that ungulates exhibit only brief reactions to overflights. Heart-rates return to baseline levels within 2 to 3 min of an overflight by military jet aircraft (Krausman et al. 1993, Weisenberger et al. 1993). The behavioral responses of caribou to overflights by low-altitude jet aircraft also are short-term (Murphy et al. 1993). Caribou decreased lying and underwent more energetically costly activities, such as feeding or standing, at least in the post-calving and insect seasons. Whereas short-term responses to aircraft overflights are apparent, longer-term responses also may occur. Long-term responses may include an increase in daily movements and habitat shifts (Stockwell et al. 1991, Bleich et al. 1990, 1994), an increase in predation (Harrington and Veitch 1992) and, ultimately, a decline in the population. This thesis addresses aspects of longer-term responses in activity patterns and daily movements of a population of caribou overflown by military jet aircraft.

Our findings of short-term responses of caribou to low flying jet aircraft (Murphy et al. 1993) partially support those of Davis et al. (1985) who found no effect of overflights on productivity of caribou of the Delta herd. Effects of overflights were not measured directly in the study by Davis and coworkers, and their conclusions were based on comparisons between overflown and nonoverflown herds. Additionally, differences in productivity among herds could be equally attributable to limiting and regulating environmental factors rather than overflights by jet aircraft. In a more direct measure of effects of overflights by military jet aircraft, Harrington and Veitch (1992) documented lower calf survival. Bleich et al. (1990, 1994) investigated the effects of helicopter overflights on movement patterns and habitat shifts in mountain sheep. An increase in daily movements and habitat shifts had long-term ramifications due to increased encounter rates with predators (Sih 1984) and movement to habitats potentially of lower quality (Stockwell et al. 1991, Bleich 1993, Bleich et al. 1994). My thesis documents the daily changes in movements and activity patterns of caribou responding to low-altitude overflights by military jet aircraft. It does not address the implications for predation and habitat quality as these factors were not measured; however, the results show for the first time how caribou potentially habituated to low flying jet aircraft respond to repeated overflights.

I initiated the research by determining if caribou time activity to sunrise or sunset and whether they exhibit diurnal, nocturnal, crepuscular, or nychthemeral activity. An understanding of basic activity patterns is crucial to interpret possible effects resulting from anthropogenic disturbance. Data collected on activity patterns of undisturbed captive caribou at LARS and wild caribou of the Delta herd in interior Alaska showed that caribou are intrinsically nychthemeral. The following hypotheses regarding basic activity patterns of caribou were addressed in Chapter 1: (1) caribou exhibit equal activity day and night, (2) caribou do not time activity to sunrise or sunset, and (3) caribou activity patterns do not change seasonally as a consequence of daylength. For a species that times activity to sunrise, I expected to document within- and between-group synchrony (Gerkema et al. 1993), particularly at the beginning of the day when all animals began activity at virtually the same light level. Evidence of between-group synchrony should be important to management of the timing of jet overflights; for example, they could be timed to minimize disturbance. I documented clear within-group synchrony (Chapter 1, Fig. 10). Within-group synchrony has been widely documented in caribou and reindeer (Roby 1978, Boertje 1981, Skogland 1984, Dau 1986, Collins and Smith 1989, Nixon 1991, Russell et al. 1993) and may occur, regardless of whether animals time activity to sunrise or sunset, in order to enhance predator avoidance through group vigilance. Within-group synchrony is enabled through social facilitation and, probably, is not a photoperiod-driven phenomenon.

I found no evidence of between-group synchrony (Chapter 1, Fig. 8a). Between-group synchrony must be related to the cueing of activity by some environmental variable (Gerkema et al. 1993) with photoperiod being the most reliable cue (Aschoff 1960, Pittendrigh and Minis 1964, Menaker 1969, Krüll et al. 1985). Therefore, the most stringent test of light as a cue should be made in winter. I found no evidence of timing of activity (Chapter 1, Fig. 9) even though this has been suggested elsewhere (Roby 1978, Collins and Smith 1989, Russell et al. 1993). Between-group synchrony may diminish through the day as different individuals (and groups) are subjected to variable ecological factors, including forage quality and availability. Additionally, inter-individual differences in body condition may lead to divergent foraging strategies (Gaare et al. 1975, Roby 1980, Roby and Thing 1985), thereby, diminishing between-individual and between-group synchrony.

Activity of caribou in summer is said to be “free-running” (Boertje 1981, Roby 1978, Russell et al. 1993), as there is no conspicuous photoperiodic cue to standardize activity. In winter, reindeer appear to be “primarily diurnal,” and Collins and Smith (1989) concluded that reindeer time activity to sunrise, in particular, and to sunset. Timing activity to sunrise and sunset, likewise, is reported for caribou (Roby 1978, Russell et al. 1993), however, since these data sets were collected exclusively during daylight hours they do not constitute a stringent test of timing.

In Chapter 1 I argue that environmental factors such as predation by mammals and birds, harassment by insects, avoidance of heat or cold, and the availability and quality of forage exert an “ecological cost” on individuals that modify daily activity patterns. Therefore, wild populations may not be characterized by the inherent nychthemeral activity pattern and the lack of timing of activity to light documented for caribou at LARS and caribou of the Delta herd. The first clue to the effect of environmental influences on activity was a lower number of daily activity cycles for caribou of the Delta herd (4/d) compared with caribou at LARS (6/d) (Chapter 1, Fig. 5).

Thus, it was necessary to take ecological influences into account when determining the seasonal and between population effects of overflights. In particular, could the minimal effects of low flying military jets, reported by Davis et al. (1985) for the DCH and the lowered calf production reported by Harrington and Veitch (1992), be due to ecological differences between herds?

A most influential population effect on the sensitivity of individuals to overflights by jet aircraft, would be density-dependent relationships. In Chapter 2 I used activity variables to support observations that, during this study (1991), the DCH was displaying nutritional limitation, possibly in response to density-dependent effects. Nutrition can exert a strong effect on the activity patterns of ruminants (Blaxter 1962, Gaare et al. 1975, Boertje 1981, Trudell and White 1981, Roby and Thing 1985, Russell et al. 1993, Forchhammer 1995). Low quality forage results in long resting bouts as animals attempt to maximize digestion (Blaxter 1962, Hungate 1975). Many authors have suggested that activity patterns of caribou be used to estimate range quality (i.e., forage quality and forage availability) (Gaare et al. 1975, Roby 1978, Roby 1980, Boertje 1981, Roby and Thing 1985, Russell and Martell 1986, Russell et al. 1993).

In winter, caribou of the Delta herd exhibited resting bouts that were twice as long as the duration of resting bouts exhibited by caribou in 3 herds known to have access to high quality range (Boertje, 1981, 1985; Russell et al. 1993; Chapter 2). Active bout lengths were consistent among herds in winter. I attributed the longer rest period of the DCH to a low quality winter range (Fig. 15b) (Illius and Gordon 1992, Lundberg and Palo 1993, Manteca and Smith 1994, Forchhammer 1995).

In the post-calving season, caribou of the Delta herd exhibited significantly longer active bouts and equivalent resting bout lengths to the other herds (Chapter 2, Fig. 16). I concluded that availability of forage likely was low on the Delta herd range, necessitating long active bouts due to increased search time. Forage quality, in contrast, was probably equivalent to Denali and LARS caribou ranges as resting bout lengths were equivalent. Finally, caribou of the Delta herd exhibited significantly longer active and shorter resting bouts than LARS counterparts in midsummer. The short resting bout length (approximately 20% of the day) is consistent with a moderate level of insect harassment (White et al. 1975). No conclusions could be drawn with respect to nutrition in the insect season.

Results of the activity data for winter and post-calving suggest the possibility of nutritional limitation in this study year. This conclusion supports the yearly trend to decreasing body weights in 10 month old calves for this herd (Valkenburg 1993; Fig. 30). In addition, the high moss content in their diet (Table 3) supports evidence of poor winter nutrition (Valkenburg 1994). An advanced age of first reproduction and abandonment of traditional wintering and calving grounds also has been reported in years preceding the study (Fleischman 1990). This evidence suggests low nutrition, which is possibly density-dependent. I conclude that environmental and activity variables should be measured concurrently and that, under these conditions, activity data can yield extensive information regarding range condition. Moreover, the apparent low nutritional plane of Delta herd caribou in the year of this study could magnify the disturbance effects of low-altitude overflights by military jet aircraft.

Finally, I determined the effects of low-altitude overflights by military jet aircraft on activity and movements of caribou (Chapter 3) and, additionally, the energetic consequences of these overflights (Chapter 4). Terming an anthropogenic event a "disturbance" is problematic unless there is a way to quantify the extent to which an animal perceives the event as a disturbance. If there was an activity, movement, or energetic consequence to overflights, I concluded that overflights do constitute a disturbance.

I used the IEC model developed by Fancy and White (1985) to translate activity budgets into an energy cost. IECs then were related to Wildlink activity counts. Additionally, IEC was converted to ADMR, using seasonal measures of RMR from Fancy (1986). In late winter, caribou responded to overflights by increasing the daily number of resting bouts, they did not, however, move from the impact area or otherwise increase activity, IEC, or ADMR (Fig. 29). Thus, reactions to overflights were mild and do not constitute a disturbance in late winter.

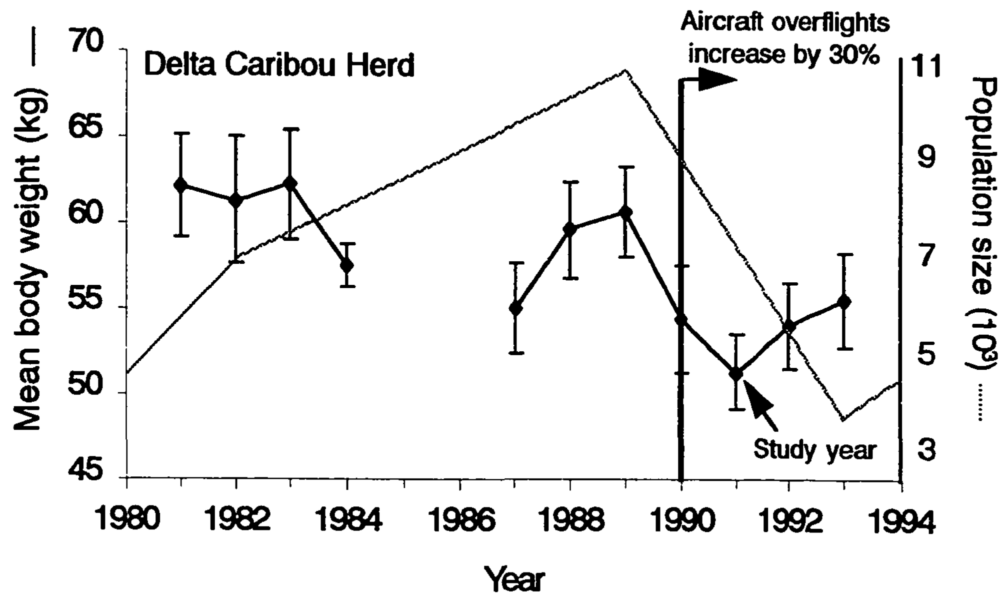

Fig. 30 Mean (± SE) body weights (kg) of 11-month-old female caribou and population size of the Delta Caribou Herd in relation to aircraft overflights in Alaska.

In post-calving caribou, instantaneous behavioral responses reported by Murphy et al. (1993) were accompanied by an increase in daily activity and an increase in linear movements in response to overflights (Fig. 24). The increased linear movement exhibited by post-calving caribou may have implications for both food intake and predation during this critical period. As a minimal effect, the caribou may be attempting to leave the impact area. IEC and ADMR significantly increased following overflights and the increases were positively correlated with the loudest overflight of the day (Table 8). Thus, overflights had a direct impact on the energetics of post-calving animals and could force animals to use poorer habitat after they leave the impact area. I recommend that military jets avoid caribou during calving and post-calving seasons as these overflights constitute a disturbance.

Evidence for overflights constituting a disturbance was equivocal in the insect season. Activity levels increased significantly in response to overflights (Fig. 22) but there was no corresponding increase in linear movements (Fig. 24) or in IEC and ADMR (Fig. 29). Even mild insect harassment is known to have an important effect on caribou energetics (Fancy 1986) and any increase in disturbance at this time could have multiplicative effects on productivity (White 1983). Insect harassment is implicated in lowering growth rates of calves of arctic caribou and in lowered conception rates of their mothers (Gerhart 1995). In this study, the energetics of this effect must be reevaluated as the RMR used to calculate ADMR was determined using caribou in good condition at LARS (Fancy 1986). Caribou of the Delta herd were in poorer condition.

Management Implications

Based upon the results presented in this thesis, I cannot make any specific recommendations in regard to daily timing of jet training exercises as caribou are active equally day and night and do not exhibit between-group synchrony. Consequently, any time, day or night, is potentially an important feeding time for individual groups of caribou. I recommend avoiding caribou during the cool of the day in the insect season as this may be a critical feeding time during that season. Finally, I recommend that calving and post-calving caribou be avoided altogether.

The nutritional status of caribou of the Delta herd was low in the year of the study. This observation is based on daily activity patterns of undisturbed caribou and is supported by independent observations that body weights of 10 month old calves were at the lowest point ever recorded. Preceding this study, population size of the DCH was declining and reached its lowest point in 1992. In addition, caribou of the Delta herd abandoned traditional wintering ranges and calving grounds. In 1990, the number of low-altitude overflights by military jet aircraft increased by 30%, coincident with population size and body weight declines (Fig. 30). Obviously, I cannot point to cause and effect in this instance, however, it behooves us to question the effects of overflights and the extent to which overflights constitute a disturbance on a potentially nutritionally stressed herd.

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