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**ENERGY EXPENDITURES OF CARIBOU RESPONDING TO
LOW-ALTITUDE JET AIRCRAFT**

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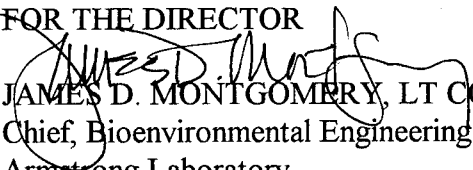
The experiments reported herein were conducted according to the "Guide for the Care and Use of Laboratory Animals," Institute of Laboratory Animal Resources, National Council.

This report has been reviewed by the Office of Public Affairs (PA) and is releasable to the National Technical Information Service (NTIS). At NTIS, it will be available to the general public, including foreign nations.

This technical report has been reviewed and is approved for publication.


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INTRODUCTION

Use of low-flying jet aircraft for military training has caused concern for the effects of these overflights on wildlife. Northern residents and resource-management agencies have concerns for the effects these training exercises may have on productivity of caribou (*Rangifer tarandus*) (Wadden 1989). Response to these concerns, coupled with National Environmental Policy Act (NEPA) requirements for military exercise, prompted the U.S. Air Force (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 research program was designed in response to a workshop task and was subsequently selected for funding by the USAF Noise and Sonic Boom Impact Technology (NSBIT) program. Caribou (*R. t. granti*) from the Delta Herd in interior Alaska were selected for study primarily because detailed energetics models were available for this species and because this herd occurs near Eielson Air Force Base in Interior Alaska.

The effects of disturbance by military aircraft on the behavior of caribou are reviewed in a companion report (Murphy *et al.* 1993). Results presented by Murphy *et al.* (1993) address field objectives of this study:

- 1) to measure the noise exposure experienced by caribou overflown by jet aircraft;
- 2) to record behavioral reactions of caribou to overflights by low-altitude jet aircraft by direct observation;
- 3) to record activity cycles and movements of caribou exposed to overflights by low-altitude jet aircraft using telemetry; and
- 4) to evaluate the behavioral responses of caribou to overflights as a function of noise exposure.

The telemetry data (objective 3) were evaluated for their energetic and population productivity implications using computer simulations and prediction equations based on tame caribou and reindeer (*Rangifer tarandus tarandus*) at the Large Animal Research Station (LARS), Institute of

Arctic Biology, University of Alaska Fairbanks. This report details the rationale, objectives, results and implications of this analysis.

The rationale for linking empirical behavioral and energetic responses of caribou from field and laboratory studies to computer simulation of population responses, is based on the assumption that the effects of a stressor, in this case a dose of sound from a low-altitude jet aircraft, on a given wildlife population could be expressed at the population level if the stressor is significantly disruptive to the time/energy budget of the animals. However, such responses can be empirically measured only in long-term studies, often placing a costly chronic impact on the exposed (treatment) population. A predicted measure of population response can be derived through modeling. Such models are driven by factors that affect energy intake and energy expenditure of individuals, while energy flow through populations, and the effect of energy limitation on population productivity, are intermediate variables and output of the model.

Energy expenditure and activity energy costs are well documented for caribou (White and Yousef 1978; Fancy and White 1985; Fancy 1986; White and Fancy 1986) and the effect of energy and nutrition on fecundity is known quantitatively (Cameron *et al.* 1993; Gerhart *et al.* 1993). In addition, seasonal energy budgets of caribou have been assessed from an evolutionary and ecological perspective (White *et al.* 1975; Boertje 1981, 1985; White 1983; Fancy 1986; White and Fancy 1986; Klein *et al.* 1987; Russell *et al.* 1993) and this knowledge provides a strong framework with which to assess disturbance impacts. The effects of disturbance on caribou varies depending on type of disturbance, time of year and animal group (nursery bands, bull groups, mixed aggregations) (Gunn *et al.* 1985; Murphy and Curatolo 1987; Harrington and Veitch 1991, 1992). This information has been used to develop a caribou energetics model (CARIBOU) that links animal activity and habitat-forage data to the annual body condition cycle, the milk production and calf growth rate for caribou (Hovey *et al.* 1989a; Kremastar *et al.* 1989; Kremastar 1991; Russell 1991; White 1991; Daniel 1993; Russell *et al.* 1993). In the present study, annual energy

budgets of female caribou were simulated and the effects of jet overflights (Murphy *et al.* 1993) were assessed in terms of reproductive output (Luick and White 1994). Computer simulations also incorporated a wide array of influencing variables, such as weather and parasitic insects.

The first step in the modeling process was to develop an independent measure of energy expenditure for use in the field. We evaluated the use of heart-rate monitoring (Fancy and White 1986) and conversion of daily activity budgets to an energy budget (Hudson and White 1985; Fancy and White 1985) as techniques to quantify average daily metabolic rate (ADMR) and the incremental energy cost (IEC) of activity associated with field existence. Under natural conditions, animals are frequently out of sight, and it is impossible, therefore, to determine the daily activity budgets of free-ranging caribou by direct observation. We used remote sensing of activity by a mercury tilt-switch, fitted to a data acquisition and transmission system, built into a caribou neck-collar (*Wildlink* activity system). We then converted *Wildlink* activity counts to IECs and ADMR using the daily activity budget. Conversion, or calibration, equations were constructed using tame animals at LARS.

Even under ideal circumstances, when energy expenditure could be predicted from *Wildlink* collar output in response to overflights, these results cannot be interpreted directly in relation to measures of animal performance such as conception rate, calf survival and calf growth rate. The approach can, however, be used to assess an immediate energy cost, that may be evaluated in-turn for its effect on these population parameters through computer simulation modeling.

In this modeling exercise, we assumed that the effects of sound exposure could be translated to animal productivity through a decrease in time spent lying and an increase in time spent active (Murphy *et al.* 1993). Because we could not allocate time spent in each component of the active period, foraging (eating and searching), walking or running, we made the explicit assumption that disturbance by jet aircraft did not change the time distribution within the active period. Therefore,

it is implicit that caribou could, and did, make a compensatory increase in time spent foraging, and feeding, which is a finding for caribou disturbed by transportation corridors (Murphy and Curatolo 1987). This compensatory feeding could offset energetic costs associated with an increase in activity. We then used computer simulations to explore the hypothesis that increased time spent active was attributable to walking and that no compensatory feeding occurred, i.e., time was spent "searching" for food rather than "eating" forage.

To simulate effects of low-flying jet aircraft, it was necessary to add two major subroutines to an existing model: Computer Simulation Models for the Porcupine Caribou Herd (CARIBOU Version 2.0) belonging to the Canadian Wildlife Service, Whitehorse, Yukon Territory (Kremsater *et al.* 1989). One subroutine allowed daily input of the number of jet overflights and the expected single event noise exposure level (SEL, dBA) of each overflight. SELs were summed to give a daily "dose" of sound termed the Time Average Sound Level (L_T , dBA). L_T then was used to modify the model activity budget, termed the default activity budget, for that day using both a simple change in time spent resting and subsequent change to the active component. The model then generated the body weight and fat level at mid-rut for a treatment (i.e., overflown) and control (non-overflown) animal. Body fat levels were used to generate fecundity parameters using a second subroutine. The fecundity subroutine estimated probability of conception of control and treatment simulations. For treatment runs, the projected change in conception rate from control, or the absolute predicted conception rate, then was printed out for the user to determine if a given scenario had implications for initial fecundity, a major variable affecting population dynamics of caribou.

A major problem with modeling the effects of jet overflights on a single female, which may or may not be pregnant or lactating, is whether the female is exposed to the SEL of each overflight. In the model, the user can stipulate the probability (0-1) that the animal will be exposed to sound for each overflight. If the probability is 1 then this gives a deterministic output. However, the model also

can allocate a random number between 0, no sound exposure, to 1, full SEL at the animal, which is used to give a stochastic output. The latter is relevant to scenarios that evaluate the effect of many possible overflights on a single animal.

A description of the simulation modeling process is given in a manual, *Computer Simulation Model for Jet Aircraft Disturbance of Free Ranging Caribou* (Luick and White 1994), which accompanies an executable version of the CARIBOU model.

Goals and Objectives

The goal of this research program was to assess the energy costs of responses of caribou to overflights by low-altitude, subsonic jet aircraft and to incorporate these findings into a model to predict general energetic and demographic consequences of repeated overflights. In this report, we present: a) our determination of energy expenditure using heart rate monitoring, b) results of our laboratory research on calibration of *Wildlink* activity monitoring collars with IEC and ADMR assessed behaviorally, c) estimates of IEC and ADMR of caribou in response to jet aircraft disturbance and, d) model assessment of demographic consequences of repeated jet overflights. Results of behavioral studies are presented in a separate report (Murphy *et al.* 1993), and a description of the model and its use for simulation is presented in a manual (Luick and White 1994). Specific objectives were to:

- 1) evaluate the usefulness of heart-rate monitoring as a means of determining the ADMR of free-ranging caribou in the wild;
- 2) document normal seasonal, undisturbed activity patterns and daily activity budget of captive caribou in relation to *Wildlink* activity counts;
- 3) determine IECs from daily activity budgets of captive caribou;
- 4) predict energy expenditure of caribou from *Wildlink* activity counts;
- 5) estimate IEC and ADMR of wild caribou from *Wildlink* activity counts; and
- 6) assess effects of low-altitude jet aircraft overflights on caribou fecundity.

METHODS

Captive Animal Studies

Three caribou held at the University of Alaska Fairbanks Large Animal Research Station (LARS) were fitted with subcutaneously implanted heart rate transmitters developed by J. Stuart Enterprises, CA (Fancy and White 1986). For this system, each heart beat is detected and transmitted, the transmission recorded and the number of beats/unit time, or the time between successive beats, is used to calculate a heart-rate (HR, beats/min). This system was evaluated for signal distortion and detectability while animals were carrying out typical activities. In addition, an externally mounted heart-rate monitor designed for use with race-horses and humans (Uniq Heartwatch, Computer Instruments Corporation, Hempstead NY 11550, Model 8799), was evaluated for its use in field situations. Although we have shown previously a close correlation of HR with energy expenditure (Fancy and White 1986), these relations were to be verified for typical instantaneous, or startle, responses using a treadmill fitted with a head-stall (Fancy and White 1986; Luick and White 1994; Floyd 1987) or a confinement chamber (Frisby and White 1984) to determine gaseous exchange. Such animals must be well trained so as to minimize background "noise." On three occasions field estimates of HR were recorded from a caribou fitted with the *Wildlink* activity collars that simultaneously were observed for estimation of the daily activity budget.

In order to interpret activity counts from *Wildlink* collars, and to convert activity counts to IEC and ADMR, it was necessary to document the daily time-activity budgets. Twenty-six hour behavioral observations were conducted once monthly on 3 captive male caribou and 3 female caribou and their calves at LARS using focal-animal, all occurrence sampling (Altmann 1974). Recorded behaviors included: lying, standing, feeding, grazing, drinking, cratering, antlering, walking, running, playing, and nursing. Caribou were housed in pens ranging from 0.1 to 3 ha. Observers in towers watched caribou and recorded behaviors using a laptop computer with a

Observers in towers watched caribou and recorded behaviors using a laptop computer with a program written for this purpose (DIAP; LARS). Initial behaviors were recorded for all focal animals at the onset of each observation period; thereafter, each new entry was made as the animal started a new behavior. *Wildlink* activity counts were collected concurrently by downloading the number of counts accrued each 10, 30 or 60 min during the 26 h study period.

Output from each 30 min of the activity monitoring system in *Wildlink* collars was related to the behavior(s) of the caribou observed for the same time-period. *Wildlink* collars have an activity monitoring system composed of a mercury tilt-switch and a computer chip that collects and stores the number of tilts accumulated during 36 equal-length intervals (ranging in length from 1 to 90 min). Activity was recorded by a mercury tilt-switch that registers a count (i.e., activity count, AC) each time the collar was tilted. A triggering transmitter is used to signal the collar, the collar responds by transmitting stored data in binary code which is received using a standard Telonics receiver, recorded by hand, and later translated (Mech *et al.* 1990; Kunkel *et al.* 1991). *Wildlink* collars were programmed to collect ACs in 30 min (AC_{30} , January through April 1991) and 10 min (AC_{10} , May 1991 through end of study) intervals.

Caribou behaviors were translated into an incremental energy cost (IEC) using energetic costs of activity relative to lying (Fancy and White 1985, 1987) (Table 1). Relative cost of each activity (e.g., 1.24 for standing) was multiplied by the time spent in that activity. These values were summed over a 30- or 60-min interval to yield the IEC_{30} or the IEC_{60} , respectively. IECs and ACs were plotted through time to determine relationships between IEC and AC. Mean IEC for 24h (IEC_{24}) was estimated as the sum of $IEC_{60}/24$.

Table 1. Incremental costs of activities over resting metabolic rate for caribou.

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

Data are from Fancy and White (1985).

Relationships between IEC_{60} and AC_{60} were assessed using simple linear regression (Kitchens *et al.* 1993). Equations were developed for each caribou during each month. Analysis of covariance was used to test for effects of month, animal, or sex on regression coefficients (Zar 1984).

Elevations were tested when slopes were homogeneous. When both slopes and elevations were homogeneous, data were pooled and an overall equation developed.

ADMR ($\text{kJ/kg}^{0.75}$) of each caribou was estimated as:

$$\text{ADMR} = IEC_{24} * \text{RMR}$$

where RMR = daily resting metabolic rate ($\text{kJ/kg}^{0.75}$) measured for captive caribou (Fancy 1986) after correcting for body weight of each caribou. RMR is the metabolic rate of fully-fed caribou while lying and ruminating.

Energy Costs and Metabolism of Overflown Caribou

During each study season, IEC_{60} for each *Wildlink* collared caribou was estimated from the relation of AC_{60} versus time (Kitchens *et al.* 1993), as detailed by Murphy *et al.* (1993) and the seasonally

appropriate relationship between IEC_{60} and AC_{60} as derived from laboratory studies. Data were available for both control and treatment caribou.

ADMR of each caribou for each day of the field study was estimated by the same equation as for the LARS studies:

$$ADMR = IEC_{24} * RMR$$

where RMR is the seasonally adjusted daily metabolic rate ($\text{kJ/kg}^{0.75}$) for a fully fed caribou while lying and ruminating taken from Fancy (1986); namely 718 in late-winter, 942 for post-calving and 895 for the insect season. Female caribou were assumed to be pregnant in late-winter, and lactating in the post-calving and insect seasons.

To determine effects of aircraft noise on IEC_{24} and ADMR, linear regression models (SAS-all possible models) were developed using data from animals subjected to low-altitude overflights by jet aircraft in the field. Specifically, we wanted to determine which noise variables, if any, were important in explaining the variation in IEC_{24} and ADMR. Independent variables considered were: 1) number of overflights ≥ 85 dBA (NF), 2) loudest overflight each day (LOUDSEL), and 3) average sound exposure for the treatment day (L_T). Significance was assessed at $P < 0.10$ level because of small sample sizes.

Simulation of Overflights on Caribou Energetics and Fecundity

Before the caribou energetics model could be used to meet the goals and objectives of this study it was necessary to write two bridging subroutines; one subroutine modified daily activity data and the other transferred body weight and fat levels to a measure of probability of conception (i.e., fecundity). The energy model operates on a one day time-step and derives an energy expenditure based on seasonal time-activity budgets for caribou. The activities of the time-activity budget include time spent lying (L), standing (S), walking (W), running (R), and foraging (F). Foraging time also was broken down into the fraction spent eating (E) and that spent pawing (P) for food

through snow. This budget can be summed to give active ($W + R + F$) and rest ($L + S$) cycles. We have shown previously (Kitchens *et al.* 1993; Murphy *et al.* 1993) that active and rest cycles can be detected remotely using the mercury tilt switch in *Wildlink* radio-collars. Daily activity budgets for subject caribou were estimated from a synthesis of activity budgets as employed in the model CARIBOU. The structure of this PC compatible computer model was amenable to modification for aircraft disturbance simulation. Regression analysis showed that the active-rest cycle variables were related to sound exposure (Table 3 in Murphy *et al.* 1993). We found that resting duration (rest, h/d) could be predicted from the summed daily noise level exposure, L_T , in all three seasons, namely late winter, post-calving and insect. For gaming with the model we assumed this was the case for other seasons of the year.

Seasonal effects were noted for components of active and rest variables. For the greater part of the year, L and S minimally activated the mercury tip switch and were grouped together as 'resting'. The remaining activities were grouped as 'active'. However, during periods of insect harassment, S was classified within the active component as head movements of caribou raised the AC above acceptable levels for rest. The initial subroutine of CARIBOU was written to redistribute total activity among components according to the relative contribution each activity made to the rest or active variable of the default activity budgets within CARIBOU. For instance, when a simulation of a control animal did not predict running on the exposure date (i.e., fraction of the day spent running was zero), no running would occur as a result of an overflight. Likewise, if the effect of L_T was to reduce the daily active time, the amount of time spent in W, R, and F would be reduced in proportion to their contribution in the default activity budget.

To initiate a simulation run the user must complete a flow of information from a list of proposed overflights (i.e., the simulation begins by assembling a text file FLIGHT.LOG). This was accomplished using the program FLIGHT.EXE. The text file FLIGHT.LOG is a matrix of 6 columns by at least 365 rows. Column headings were Day (day of the month), Month (month of

the year), Julian Day (numeric day of the year), Sortie (consecutive overflight for that day), SEL (for that sortie) and Probability (the probability that an overflight will in fact be in the proximity of the model animal). Once this file is created, the default activity budget is retrieved and used as a reference for manipulation. Changes to the activity budget are automatically executed via a subroutine within CARIBOU. The default activity budget can draw from a series of years considered to lie between low and high stress levels for caribou depending on forage quality and availability and snow depth. For the study population, the most appropriate default activity budget, and other driving variables, were for a relatively normal year.

Recalculation of the activity budget began on Julian day 1, sortie 1 and continued through the year. For each day, L_T (dBA) was calculated according to ANSI S12.40-1990:

$$L_T = 10 \log_{10} \left[\frac{1}{21600} \sum_{i=1}^N 10^{SEL_i / 10} \right]$$

where 86400 is the seconds in the overflight period, estimated to occur between 1000 and 1600 h or 6 hours each day. As the model stepped to a new day, the occurrence of overflights was determined from the probability of an overflight or by selection of a computer generated random number in order to give a stochastic analysis. For the stochastic analysis, if the generated number (0-1) exceeded the probability of overflight (0-1), taken from FLIGHT.LOG, the overflight was ignored.

For all days except the insect season, time at rest (h) was calculated as from a modification of the appropriate equation for late winter in Table 3 of Murphy *et al.* (1993):

$$\text{Rest} = 24 * (\text{dLie} + \text{dStand}) - 0.03 * L_T$$

where dLie and dStand were the default fraction of the day in L and S. The remainder of the day was considered active. During the insect season the equation was:

$$\text{Rest} = 24 * (\text{dLie}) - 0.03 * L_T$$

The regression coefficient (0.03) was arrived at through consideration of the 3 seasons of the year for which data were available (Murphy *et al.* 1993). Once the adjusted activity budget was calculated, program control was returned to the user. Execution of CARIBOU included either the default or disturbance activity budget, thereby allowing direct comparison of overflight effects via numeric comparisons, or graphic overlays, of any or all of 83 variables retained by the model.

The simulation model CARIBOU predicted variables of a female caribou based on criteria such as predicted forage quality and availability, balancing metabolizable energy intake with energetic demands placed on the animal. Energetic demands were partitioned into costs associated with the animal's activity budget, such as foraging and locomotion, and costs of production, such as growth, gestation and lactation. The model further predicted body composition of the female throughout the year including body lean and total body fat.

The likelihood of a free-ranging caribou becoming pregnant is highly correlated with body condition during the rut, with total body fat showing the closest correlation (Gerhart *et al.* 1993). Disturbance was linked with fecundity through a logistic relationship, probability of conception and autumn fat weight. The mid-rut date of October 10 was selected to assess body condition of the modeled caribou. The probability of a pregnancy (0-1) at that date was derived by Gerhart *et al.* (1993) as;

$$\text{Probability of Pregnancy} = [1 + e^{1.249 - 0.323\text{Fat}}]^{-1}$$

where fat is amount of total body fat (kg) during mid-rut.

RESULTS

Captive Animal Studies

Those caribou that could be trained to treadmill research and for research associated with disturbance activities required four training sessions in order to enter physiological studies (Figure 1).

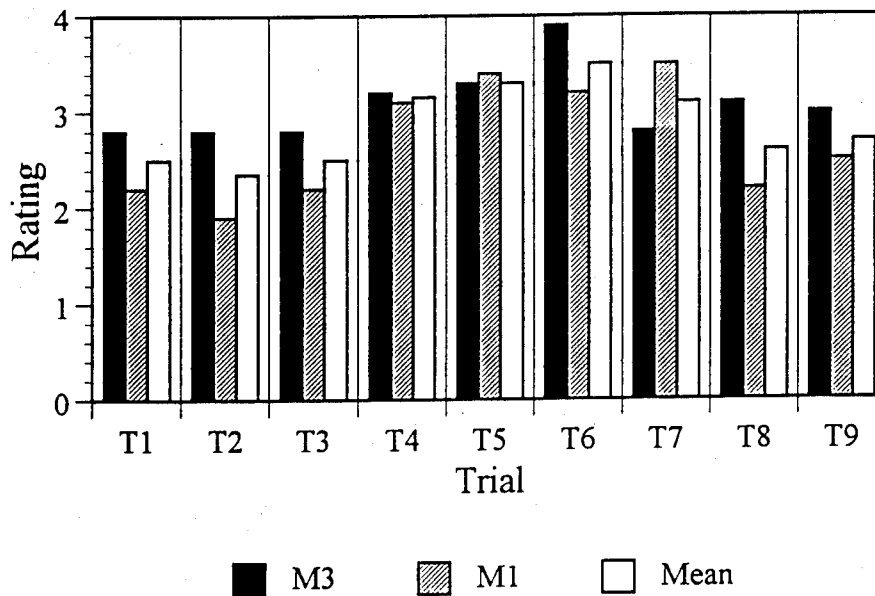


Figure 1. Change with training session in the rating of experimental tractability (Rating, 0-5) of caribou standing or walking on a treadmill. Ratings were 0, completely intractable, (i.e., will not approach, stand or walk on treadmill); 1, physical assistance needed for the caribou to approach and stand on treadmill; 2, caribou required minimal coaxing to stand on treadmill, is restrainable in headstall but will not walk; 3, caribou walks with coaxing; 4, caribou walks calmly shows occasional hesitation and gait changes; 5, completely trained caribou which walks onto treadmill stands calmly in headstall and walks without hesitation. Data are for 9 trials (T1...T9) using two male caribou using M1 and M3.

After several weeks following training sessions, caribou walked with a rating of 3 to 4. In comparison, reindeer were walking with a rating of 4 to 5 by session T5 and remained highly tractable. The most tractable caribou then were used for heart rate (HR) monitoring systems, and linking the *Wildlink* AC system with HR responses in the field.

Although both the implanted and externally mounted heart rate monitoring systems could be used to document HR of caribou, both systems suffered from defects that resulted in their rejection for field studies with wild caribou. The Stuart implanted transmitters were rejected because of reception range and their propensity to migrate beneath the skin or wear through the skin, resulting in loss of the signal, often within 2 weeks of implantation. The problem of transmitter movement was rectified by sewing the transmitter to the skin with a button on the skin's exterior surface. However, though the transmitter remained in place, the reception range was less than 300 m, the signal was lost when the animal moved behind a hill or stand of trees, and no reception was detectable when the receiver was on the opposite side of the implant. Reception from implanted transmitters was not distorted by animal movement. Signals from the transmitter occasionally failed completely when the animal was lying. The Stuart implanted transmitters also proved to be subspecies specific and had to be electronically manipulated to work on individual caribou. We could not carry out this manipulation in the field. The externally-mounted Uniq Heartwatch system was rejected because electrodes would not adhere to skin for more than a few hours, whereas field studies required 20 days of continuous operation. In addition, data storage in the Uniq Heartwatch was insufficient for the duration of the study. The unit's cold tolerance was unacceptable for use in winter. Thus, although both the Stuart implantable and the Uniq Heartwatch systems are useful for laboratory studies, they cannot be used on wild caribou in the field.

Although heart rate monitoring systems were rejected for use on wild caribou they were used to estimate resting energy expenditures (termed resting metabolic rate, RMR), IECs and daily energy expenditure patterns. The following hypotheses were tested to evaluate the association of behavioral activity and HR:

- H₀: For lying caribou, HR did not alter with head location and sudden movements of other caribou that caused startle reactions.

H₀: HR did not change with daily behavioral activity of caribou and was not related to either AC from *Wildlink* collars or IEC estimated by behavioral observations.

For free-grazing unrestrained caribou, we found a significant increase in HR while the head was elevated to the alert position when the caribou was lying (Figure 2). The head-down and head-up positions may be maintained for many minutes during a lying period. Head-up was associated with an increase of 3 to 5 beats/min over head-down, equivalent to an O₂ consumption of 48-100 ml/min, (i.e., a 10% increase in resting metabolism; Fancy and White 1986). Our attempts to confirm the oxygen cost of head position in an open flow calorimeter were not successful, and in the absence of contradictory data, we assume the head-up position is associated with a 10% increase in energy expenditure over the head-down position.

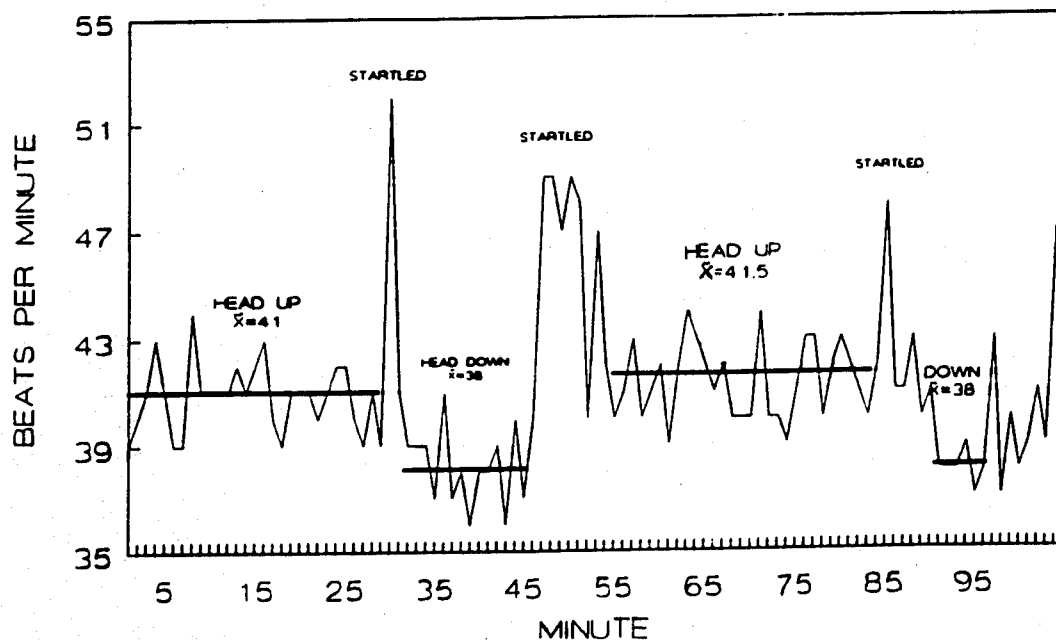


Figure 2. Heart rate responses in caribou.

Typical and mean (\bar{x}) heart rate (HR, beats/min) in relation to time (minute) of a caribou lying with head-down (i.e., 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 an implanted HR transmitter while the animal was resting in a small pasture at the Large Animal Research Station.

Caribou startled by quick movements of other animals also exhibited a marked increase in HR. However, the duration usually lasted no more than 1 to 3 min (Figure 2). Our previous studies (Floyd 1987) showed that an average startle response, similar to those in Figure 2, were associated with an oxygen consumption of 1-5 ml, equivalent to a caribou moving 1 to 3 m (horizontal distance).

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. At no time could we use the Uniq Heartwatch system for comparison with daily activity budgets. A cyclical pattern of HR through the 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 (Figure 3). Also shown in Figure 3 are the expected excursions in oxygen consumption using prediction equations of Fancy and White (1986) for a caribou of similar body weight, and IEC predicted from daily activity budget (Table 1). All 3 measures showed similarities in timing of excursions in relation to active and rest cycles. Based on these findings, we rejected the hypothesis that HR did not change with activity.

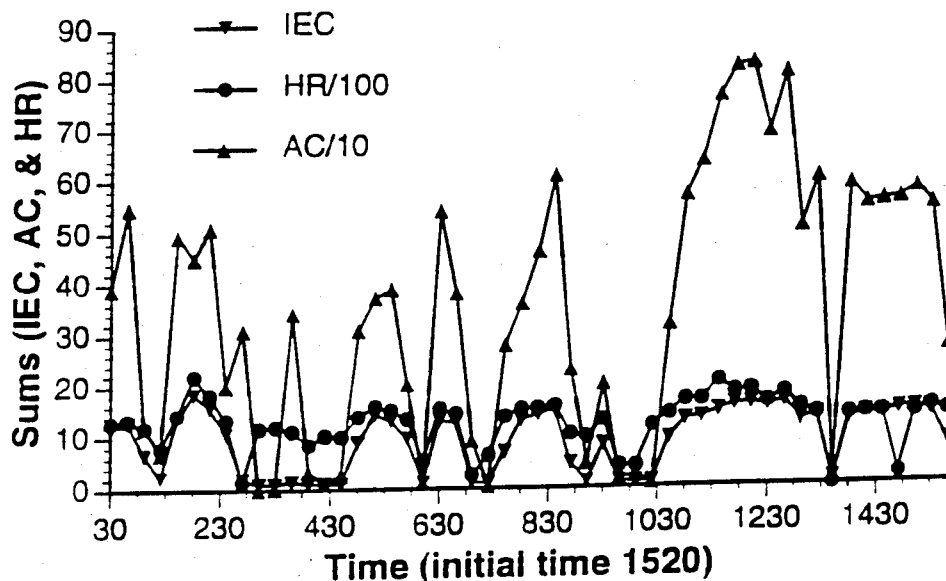


Figure 3. Association of activity counts, incremental energy cost and heart rate in caribou.

Typical daily pattern of heart rate (HR, beats/min) in relation to incremental energy cost (IEC; Fancy and White 1986) of a male caribou over a 15 h period. The caribou was fitted with an activity-monitoring radio collar (*Wildlink, Inc.*) which yielded activity counts (AC) from a mercury tip switch. AC, HR, and IEC were summed in 30-min periods and plotted through time.

We tested the feasibility 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. Models produced using simple linear regression indicated that a long time interval (i.e., 60 min) resulted in a higher amount of variation in IEC accounted for by the independent variable (AC) than seen in models produced using a short time interval (i.e., 10 or 30 min; Figure 4). Good concordance was noted in comparisons of HR, AC and IEC over intervals of 30 and 60 min (Figure 5). For both intervals, lying and active periods were clearly detectable, however, the 30 min interval yielded no extra data over 60 min. 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) more easily handled. *Wildlink* AC also enabled simultaneous collection of data on multiple animals and, for the first time, we documented group synchrony of activity in caribou (Figure 6).

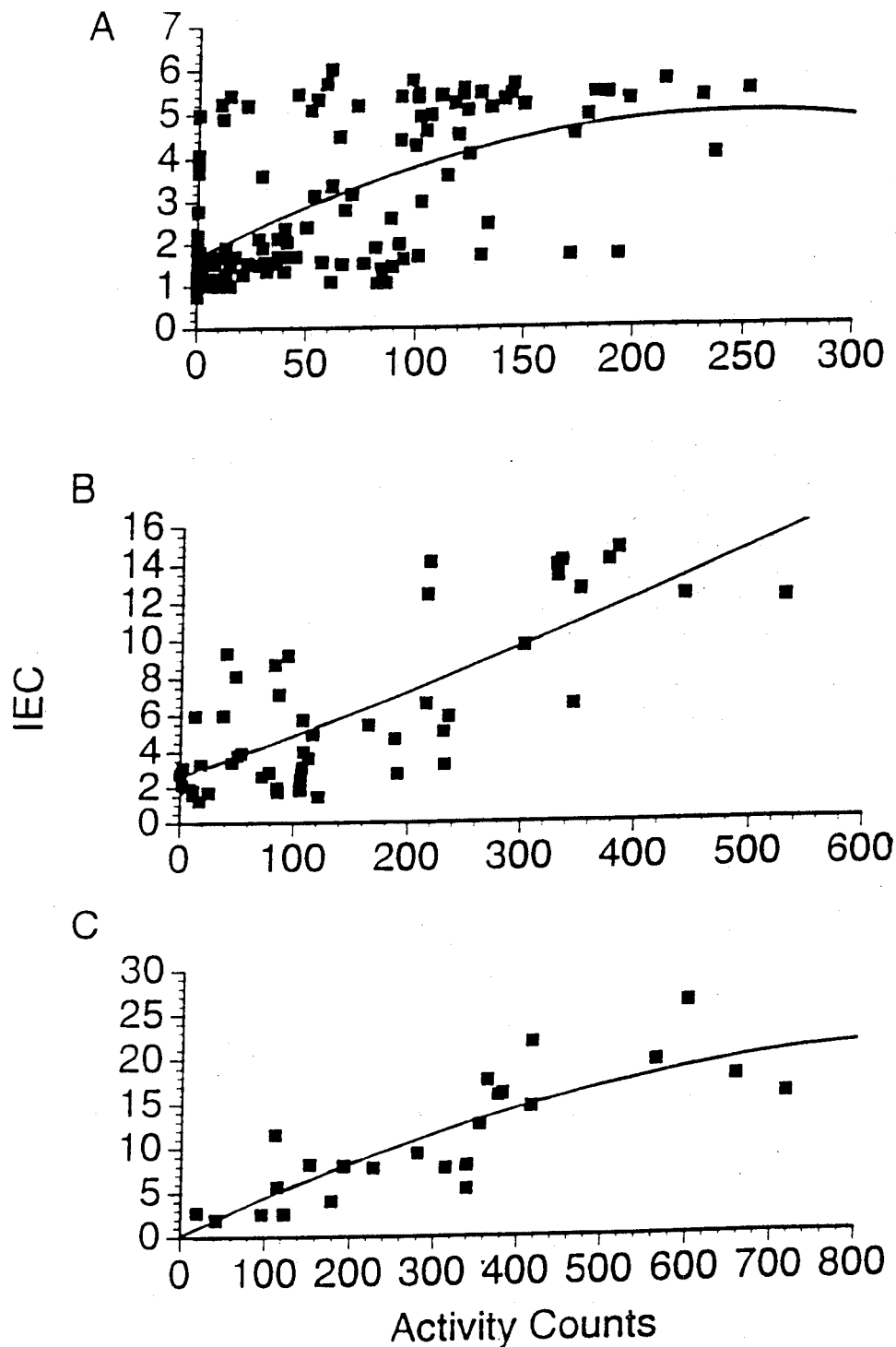


Figure 4. Correlation of incremental energy cost (IEC) with activity counts. Behavior observation collected on a caribou were translated into IEC using standardized coefficients (Table 1). IEC = energy cost of activity/energy expenditure while lying with head down. Activity counts were collected in 10-min periods from an activity-monitoring radio collar (*Wildlink, Inc.*) fitted to a neck collars. Line of best fit is shown for IEC and AC summed in (A) 10-, (B) 30-, and (C) 60-min periods.

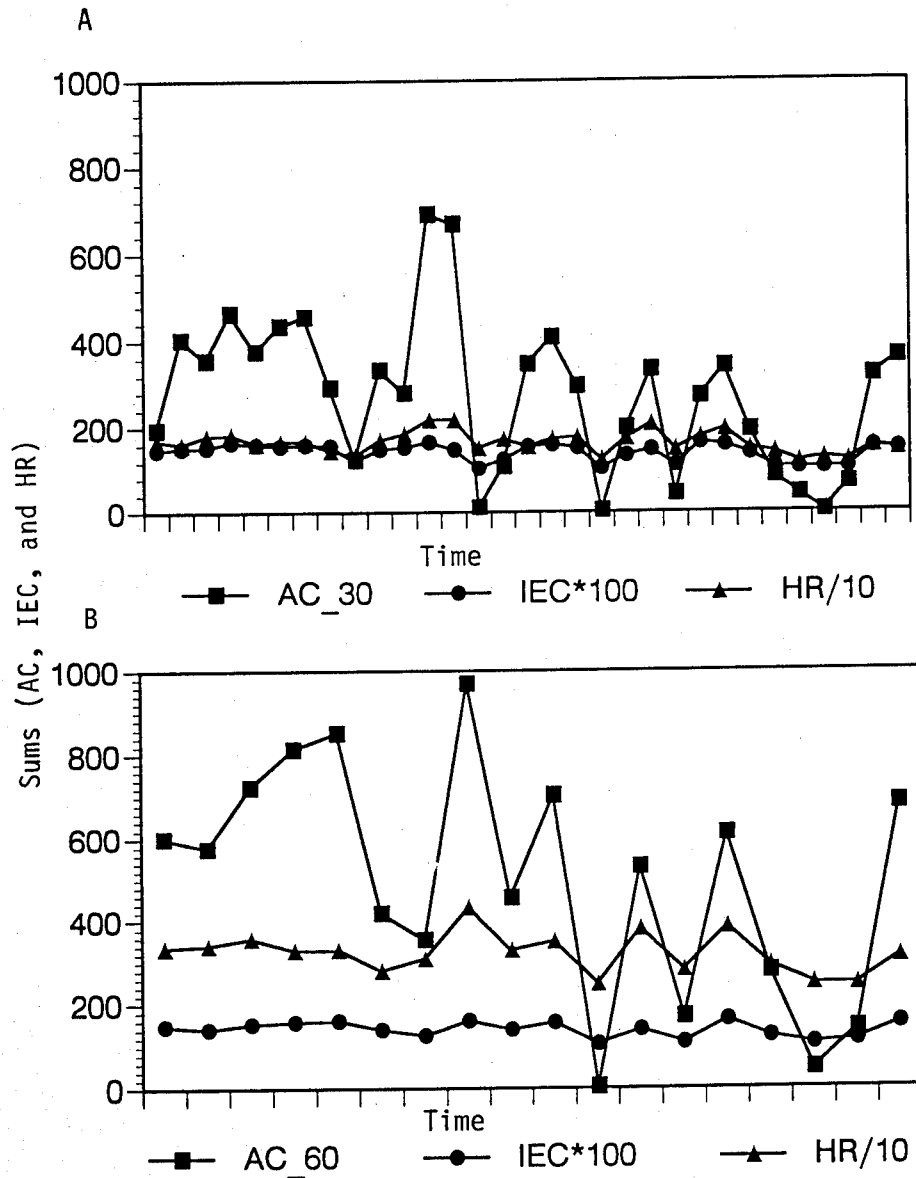


Figure 5. Effect of time interval for data summation on the associated variation in activity counts, incremental energy cost and heart rate of caribou. Behavioral observations were collected from a caribou fitted with an activity monitoring radio collar (*Wildlink, Inc.*) and a heart rate (HR) transmitter. Activity budget was converted to incremental energy cost (IEC, Table 1) (Fig. 4). Activity counts (AC), HR, and IEC were summed over 30- (A) and 60-min (B) intervals and plotted over a 24-h period.

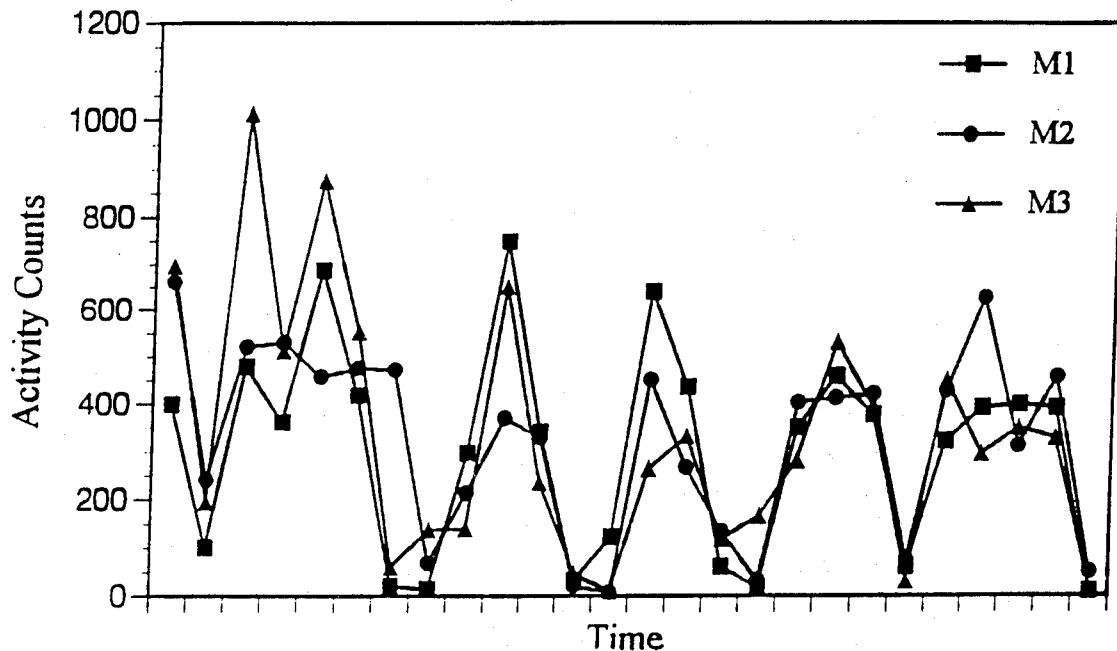
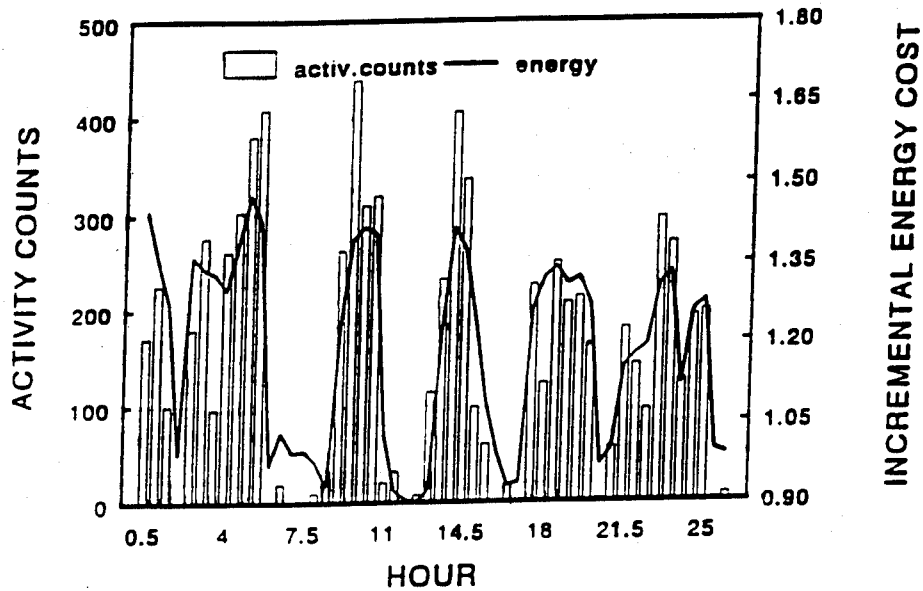


Figure 6. An example of daily synchrony of activity in caribou. Activity counts were collected from 3 male (M1, M2, and M3) and 3 female (F1, F2, F3) fitted with activity-monitoring radio collars (*Wildlink, Inc.*) and grazing a large pasture at the Large Animal Research Station. Activity counts were summed in 30-min intervals and plotted through a 26-h period.

A detailed description of the concordance of AC and IEC for two caribou is shown in Figure 7. A comparison of relationships of hourly HR and AC with IEC_{60} is shown in Table 2. In all 3 studies AC_{60} was more highly correlated with IEC_{60} than was HR. Likewise, in these studies, HR_{60} (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. Because IEC also is correlated with HR (Fancy and White 1985) the data on concordance and correlation of HR with IEC support a strong basis for extrapolation of ACs to IEC under field conditions. Also, high correlations between HR_{60} and AC_{60} (Table 3) support the use of ACs as measures of energy expenditure. Therefore, a set of empirical relations between IEC_{60} and AC_{60} were constructed through 6 months of the year at LARS (Table 4). Female and male caribou were used and relations were assessed by covariance analysis for combinability between animals and months.

18 February 1991 summaries -- M1
Incremental energy and activity counts



18 February 1991 summaries -- M3
Incremental energy and activity counts

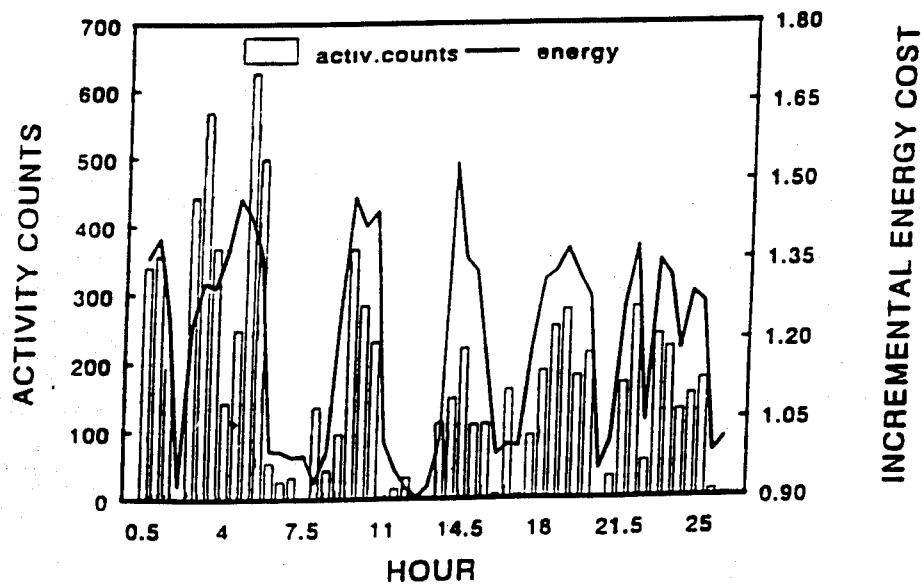


Figure 7. Concordance of hourly activity counts and incremental energy costs in caribou at the Large Animal Research Station. Data are for two males (M1, M2) feeding from a food trough and cratering through snow. See Figure 4 for definition of activity counts and incremental energy cost.

Table 2. Relationships between incremental energy cost (IEC) and heart rate (HR) or cumulative activity count (AC).

Hourly AC and HR (beats/min) were collected on male caribou during a 26-h behavioral observation period at the Large Animal Research Station. Activities of caribou were converted to an hourly incremental energy cost (IEC), Table 1). AC and HR each were compared to IEC using simple linear regression for each of 3 observation periods.

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

Table 3. Regression of heart rate (HR_{60} , beats/h) on cumulative hourly activity count (AC_{60}).

Data were for male caribou grazing a small pasture at the Large Animal Research Station. HR_{60} data were recorded from an implanted HR transmitter and AC were obtained from an activity-monitoring radio collar (*Wildlink, Inc.*).

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

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

Table 4. Regression of hourly incremental energy cost (IEC_{60}) on hourly activity counts (AC_{60}) for caribou. IEC_{60} was estimated from activity budgets and AC_{60} of captive caribou grazing in mixed sex groups in a large pasture at the Large Animal Research Station. Animals used included 3 male (M1, M2, and M3) and 3 female caribou (F1, F2, and F3).

Animal	β_0	β_1	r	SE
<u>December</u>				
M3	1.06	0.0005	0.969	0.062
<u>January</u>				
M2	1.02	0.0008	0.824	0.092
M3	1.03	0.0006	0.860	0.113
<u>February</u>				
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
<u>March</u>				
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
<u>July</u>				
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
<u>September</u>				
M1	1.05	0.0010	0.900	0.070

$IEC_{60} = \beta_0 + \beta_1 * AC_{60}$; r = correlation coefficient; SE = standard error of β . *Equations used to predict IEC for wild caribou.

In order to account for some between animal differences in AC in the set of individual regression equations relating IEC_{60} to AC_{60} (Table 4), several corrections were made to the data set by testing for influential points using the leverage technique (Neter *et al.* 1990). Outliers were removed only when they had more than 2.5 times the leverage of an average point. The equation for female caribou F3 in March was used to predict IEC_{60} s during the late-winter and in July (Table 4) for the post-calving and insect seasons of the Delta Caribou Herd (Table 4).

Energy Costs and Metabolism of Overflown Caribou

The following hypothesis was evaluated to test whether caribou altered their energy budgets in response to jet aircraft overflights.

H₀: Daily IEC and ADMR did not differ between caribou that had been exposed recently to jet aircraft overflights and animals that had not been overflown.

IEC₂₄ for animals in the control groups ranged from 1.138 to 1.286 during the 3 sampling periods (Table 5). Although IEC₂₄ was higher in 4 of 6 cases for the treatment animals by about 1-3%, only the post-calving increase was significant (P = 0.039). IEC₂₄ was similar in control animals for each season, with the highest value occurring during the insect season.

Table 5. Daily incremental energy cost (IEC₂₄) ± SEM of control and treatment (i.e., exposed to overflights by low-altitude jet aircraft) caribou in Alaska, 1991.

Season	IEC ₂₄	P
Late-Winter		
Control	1.244 ± 0.006	0.730
Treatment	1.241 ± 0.005	
Post-calving		
Control	1.281 ± 0.015	0.039
Treatment	1.335 ± 0.021	
Insect		
Control	1.286 ± 0.015	0.403
Treatment	1.318 ± 0.035	

IEC₂₄ was estimated using prediction equations shown with * in Table 4.

Estimates of ADMR for control and treatment days were not significantly different in late-winter and insect season, but ADMR on treatment days exceeded controls (P = 0.040, Table 6) during post-calving. In late winter, ADMR of control animals was lower than the following seasons (P = 0.0001) while estimates for post-calving and the insect season were almost identical (P = 0.6465).

Table 6. Comparisons of average daily metabolic rate (ADMR, $\text{kJ/kg}^{0.75}$) \pm SEM of control and treatment (i.e., exposed to overflights by low-altitude jet aircraft) caribou in Alaska, 1991.

	ADMR ₂₄	P
Late-winter		
Control	786 \pm 3.6	0.589
Treatment	783 \pm 3.1	
Post-calving		
Control	1009 \pm 11.8	0.040
Treatment	1051 \pm 16.5	
Insect		
Control	1012 \pm 12.0	0.393
Treatment	1038 \pm 27.7	

Energetic and metabolic responses of caribou to the "dose" of sound was evaluated by regressing IEC₂₄ and ADMR against the number of overflights \geq 85 dBA (NF), loudest overflight each day (LOUDSEL, dBA) and average sound exposure for the treatment day (L_T, dBA). No significant models were generated for late-winter and the insect season. For females ($P \leq 0.10$) during post-calving, however, both IEC₂₄ and ADMR increased significantly in response to LOUDSEL. LOUDSEL consistently was the sound variable with highest predictive power. All models generated with this variable are shown in Table 7.

Table 7. Response in caribou energetics to sound dose. Regression models evaluating relationships between daily incremental energy cost (IEC₂₄) and average daily metabolic rate (ADMR, $\text{kJ/kg}^{0.75}$) of caribou and the loudest sound exposure of the day (LOUDSEL, dBA) resulting from overflights by low-altitude jet aircraft in Alaska, 1991. Data were generated from equations developed on a captive female caribou (F3) at LARS (see * in Table 4).

Season	Model	r	P
<u>Late Winter</u> (n = 24)	IEC ₂₄ = 1.26 - 0.0002LOUDSEL	0.173	0.46
	ADMR = 797 - 0.119LOUDSEL	0.173	0.45
<u>Post-calving</u> (n = 32)	IEC ₂₄ = 1.14 + 0.002LOUDSEL	0.374	0.03
	ADMR = 897 + 1.52LOUDSEL	0.374	0.03
<u>Insect</u> (n = 11)	IEC ₂₄ = 1.30 + 0.0002LOUDSEL	0.141	0.69
	ADMR = 1023 + 0.156LOUDSEL	0.173	0.64

r, correlation coefficient; P, significance of r.

Simulation of Overflights on Caribou Energetics and Fecundity

The reproductive performance of caribou has been quantitatively linked to fall fat weight (Gerhart *et al.* 1993) and therefore was chosen as the basis of computer simulation projections of fecundity for caribou disturbed by noise. By adjusting the default activity budget of CARIBOU on the basis of the *Wildlink* collar results, a causal predictive model was built linking disturbance to caribou energy balance and, therefore, body fat and reproductive preparedness.

In order to check intermediary steps in CARIBOU energetics model, simulations were run on one focal animal in each season. A subsample of the data entered for this simulation is shown in Table 8. CARIBOU runs on a 1 d time step but separate lines of data, listing the overflight number (i.e., a sortie of 1 or 2 jets), the estimated SEL and the overflight probability (1.0 since the overflights were observed) are needed to calculate the mean sound dose (L_T) for each day. An initial subroutine then estimated the L_T for each day, altered the daily activity budget, and used driving variables provided in the model (i.e., default variables) to estimate IEC_{24} and ADMR (Table 9, 10).

Table 8. A typical sample of input date used to generate mean sound exposure and the daily activity data for the simulation model, CARIBOU.
Data are for one caribou, overflown in the insect season (Julian Day 211-213), in the Alaska Range, 1991.

Day	Mos	Julian Date	Sortie	SEL	Overflight Probability
01,	Jan,	1,	1,	0,	0
02,	Jan,	2,	1,	0,	0
...					
29,	Jul,	210,	1,	0,	0
30,	Jul,	211,	1,	101,	1
30,	Jul,	211,	2,	101,	1
30,	Jul,	211,	3,	97,	1
30,	Jul,	211,	4,	57,	1
30,	Jul,	211,	5,	67,	1
30,	Jul,	211,	6,	85,	1
31,	Jul,	212,	1,	95,	1
31,	Jul,	212,	2,	81,	1
31,	Jul,	212,	3,	117,	1
31,	Jul,	212,	4,	115,	1
31,	Jul,	212,	5,	115,	1
31,	Jul,	212,	6,	119,	1
31,	Jul,	212,	7,	119,	1
31,	Jul,	212,	8,	101,	1
31,	Jul,	212,	9,	88,	1
31,	Jul,	212,	10,	119,	1
01,	Aug,	213,	1,	80,	1
01,	Aug,	213,	2,	96,	1
01,	Aug,	213,	3,	94,	1
01,	Aug,	213,	4,	95,	1
01,	Aug,	213,	5,	83,	1
01,	Aug,	213,	6,	96,	1
01,	Aug,	213,	7,	96,	1
01,	Aug,	213,	8,	114,	1
01,	Aug,	213,	9,	114,	1
01,	Aug,	213,	10,	114,	1
01,	Aug,	213,	11,	114,	1
01,	Aug,	213,	12,	85,	1
01,	Aug,	213,	13,	95,	1
01,	Aug,	213,	14,	104,	1
01,	Aug,	213,	15,	100,	1
01,	Aug,	213,	16,	104,	1
01,	Aug,	213,	17,	103,	1
01,	Aug,	213,	18,	101,	1
02,	Aug,	214,	1,	0,	0
...					
31,	Dec,	365,	1,	0,	0

SEL, sound exposure level measured directly by an animal noise monitor or by extrapolation from an estimate of the slant distance (line of sight) between jet aircraft and caribou.

Table 9. Simulated effects of jet overflights on daily activity and energetics of female caribou in a normal year.

Intermediary variables in the model CARIBOU were based on non-overflown (C, control) and overflown (T, treatment) caribou in 3 study periods. Input data were for animals with radio-frequencies 150.565 in late-winter and the insect season and 150.295 when post-calving.

Season	Day	Daily Activity Budget						Activity Cycle ^a			
		L _T	Forage	Lie	Stand	Walk	Run	Active	Rest	IEC ₂₄	ADMR
Late Winter											
C	91	0	0.465	0.410	0.035	0.085	0.005	0.555	0.445	1.205	1071
T	91	55	0.520	0.347	0.030	0.095	0.006	0.621	0.377	1.236	1073
C	92	0	0.465	0.407	0.035	0.088	0.005	0.558	0.442	1.202	1069
T	92	65	0.530	0.332	0.028	0.100	0.005	0.635	0.360	1.237	1072
C	93	0	0.466	0.405	0.034	0.091	0.004	0.561	0.439	1.199	1067
T	93	56	0.520	0.341	0.029	0.102	0.005	0.627	0.370	1.228	1070
C	94	0	0.466	0.402	0.034	0.094	0.004	0.565	0.436	1.196	1065
T	94	86	0.550	0.303	0.026	0.111	0.005	0.666	0.329	1.240	1069
C	95	0	0.466	0.399	0.034	0.097	0.004	0.567	0.433	1.193	1063
T	95	82	0.546	0.305	0.026	0.114	0.004	0.664	0.331	1.234	1067
Post-Calving											
C	161	0	0.424	0.367	0.010	0.189	0.010	0.623	0.377	1.171	888
T	161	84	0.48	0.260	0.007	0.242	0.012	0.734	0.267	1.209	906
C	162	0	0.411	0.362	0.010	0.207	0.010	0.628	0.372	1.172	912
T	162	66	0.450	0.277	0.008	0.255	0.011	0.716	0.285	1.205	917
C	163	0	0.398	0.356	0.010	0.225	0.010	0.634	0.366	1.174	932
T	163	59	0.430	0.279	0.008	0.272	0.011	0.713	0.287	1.204	938
C	164	0	0.385	0.351	0.010	0.244	0.010	0.639	0.361	1.176	950
T	164	68	0.422	0.263	0.008	0.296	0.011	0.729	0.271	1.209	956
Insect											
C	211	0	0.472	0.145	0.176	0.158	0.048	0.855	0.145	1.217	893
T	211	62	0.490	0.038	0.170	0.206	0.075	0.941	0.038	1.289	946
C	212	0	0.481	0.145	0.172	0.156	0.046	0.855	0.145	1.215	887
T	212	82	0.528	0.001	0.154	0.215	0.077	0.974	0.001	1.304	952
C	213	0	0.489	0.145	0.168	0.154	0.044	0.855	0.145	1.213	880
T	213	177	0.532	0.009	0.153	0.209	0.073	0.967	0.009	1.297	941

^a, represents the fraction of day spent active and resting analogous to the daily activity cycle from *Wildlink* ACs; L_T, mean daily sound exposure (dBA); IEC₂₄, daily incremental energy cost (cost activities/resting metabolism); ADMR, average daily metabolic rate (kJ/kg^{0.75}).

Table 10. Simulated effects of jet overflights on daily activity and energetics of female caribou in a year with deep snow and high insect harassment. Intermediary variables in the model CARIBOU were based on non-overflown (C, control) and overflown (T, treatment) caribou in 3 study periods. Input data were for animals with radio-frequencies 150.565 in late-winter and the insect season and 150.295 when post-calving.

Season	Day	Daily Activity Budget						Activity Cycle ^a		IEC ₂₄	ADMR
		L _T	Forage	Lie	Stand	Walk	Run	Active	Rest		
Late Winter											
C	91	0	0.470	0.455	0.035	0.035	0.000	0.510	0.490	1.231	1057
T	91	55	0.532	0.394	0.030	0.040	0.000	0.572	0.424	1.246	1067
C	92	0	0.471	0.454	0.034	0.035	0.000	0.512	0.488	1.220	1065
T	92	65	0.545	0.381	0.029	0.041	0.000	0.586	0.410	1.242	1073
C	93	0	0.473	0.453	0.033	0.036	0.000	0.574	0.526	1.211	1072
T	93	56	0.536	0.391	0.028	0.040	0.000	0.576	0.419	1.227	1078
C	94	0	0.474	0.452	0.032	0.036	0.000	0.516	0.464	1.202	1078
T	94	86	0.570	0.355	0.025	0.043	0.000	0.613	0.380	1.235	1084
C	95	0	0.475	0.451	0.031	0.036	0.000	0.518	0.482	1.193	1085
T	95	82	0.568	0.359	0.025	0.043	0.000	0.611	0.384	1.224	1088
Post Calving											
C	161	0	0.364	0.314	0.010	0.298	0.015	0.676	0.324	1.214	889
T	161	84	0.403	0.188	0.006	0.384	0.019	0.806	0.194	1.262	925
C	162	0	0.351	0.291	0.010	0.335	0.016	0.699	0.301	1.226	904
T	162	66	0.375	0.188	0.007	0.412	0.019	0.806	0.195	1.267	935
C	163	0	0.338	0.268	0.010	0.371	0.017	0.722	0.278	1.239	917
T	163	59	0.356	0.173	0.007	0.445	0.020	0.821	0.180	1.277	946
C	164	0	0.325	0.245	0.010	0.407	0.018	0.745	0.255	1.252	929
T	164	68	0.345	0.140	0.006	0.489	0.021	0.855	0.146	1.294	961
Insect											
C	211	0	0.461	0.145	0.170	0.164	0.054	0.855	0.145	1.203	944
T	211	62	0.476	0.039	0.165	0.217	0.085	0.943	0.039	1.274	1000
C	212	0	0.470	0.145	0.167	0.161	0.051	0.855	0.145	1.201	937
T	212	82	0.515	0.001	0.149	0.226	0.087	0.977	0.001	1.288	1005
C	213	0	0.480	0.145	0.163	0.159	0.049	0.855	0.145	1.199	929
T	213	77	0.520	0.009	0.148	0.219	0.082	0.969	0.009	1.280	994

^a, represents the fraction of day spent active and resting analogous to the daily activity cycle from *Wildlink* ACs; L_T, mean daily sound exposure (dBA); IEC₂₄, daily incremental energy cost (cost activities/resting metabolism); ADMR, average daily metabolic rate (kJ/kg^{0.75}).

Figure 8 shows the approach used to repartition activity budgets in the late-winter and post-calving seasons as a result of noise disturbance. The regression of hours spent resting on L_T was used to reduce hours (negative slope) spent at rest (lying and standing) and increase hours spent active. Hours were removed from donor activity classes proportionate to class size and similarly added to the recipient classes.

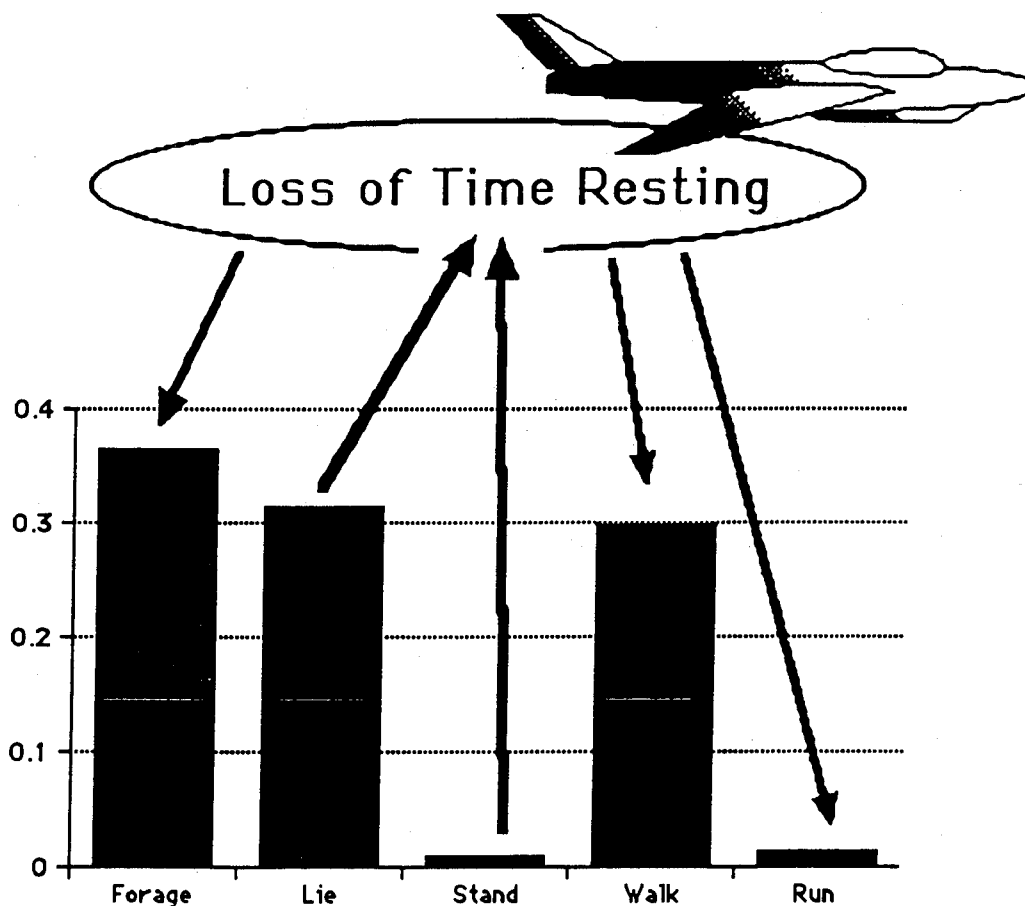


Figure 8. Repartitioning of activity budgets as results of noise disturbance. Time was taken from resting activities (lying and standing) and proportionately redistributed to the remaining activities using an algorithms relating activity with sound dose (Luick and White 1994).

While a simulation is being executed, CARIBOU displays up to 16 variables (panes) in graphic format, as shown in Figure 9. The 16 panes were selected from among 83 available variables, vertical axes are individually set while the horizontal axes represent Julian days. In this example,

the flight input file was based on a hypothetical flight schedule of 40 consecutive days of overflights beginning on day 170 and the simulation was conducted using good environmental conditions. Consecutive runs may be overlaid for direct comparisons of such effects as environmental conditions and flight schedules.

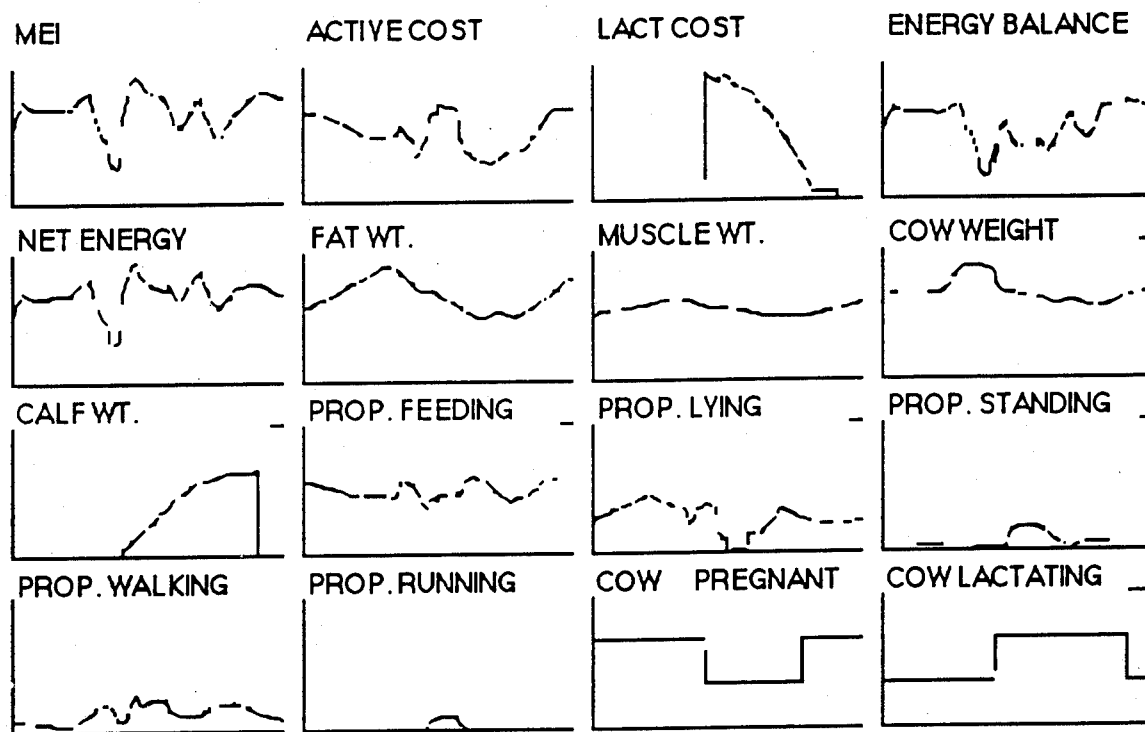


Figure 9. Intermediate variables simulated by the model CARIBOU. Typical output is shown for a one-year simulation commencing January 1. Vertical scales are independently set, horizontal scale is date. Variables assessed by model include:

MEI, metabolizable energy intake
 ACTIVE COST, daily energy cost of activity
 LACT COST, daily energy output in milk
 ENERGY BALANCE, metabolizable energy intake--(energy expenditure)
 NET ENERGY, energy available for production
 FAT WT., weight of body fat
 MUSCLE WT., weight of total lean
 COW WEIGHT, body mass
 CALF WEIGHT, body mass
 PROP. FEEDING, proportion of day spent feeding
 PROP. LYING, proportion of day spent lying
 PROP. STANDING, proportion of day spent standing
 PROP. WALKING, proportion of day spent walking
 PROP. RUNNING, proportion of day spent running
 COW PREGNANT, Julian days when pregnant
 COW LACTATING, Julian days when lactating

Intermediary output included daily L_T , activity budget including the probable active-rest cycle and ADMR and IEC_{24} for scenarios representing a normal (Table 9) and a bad (Table 10) year. For both scenarios, the model predicted that for L_T ranging from 55 to 86 dBA caribou responded with a consistent increase in activity at the cost of rest which increased time spent foraging and walking with a compensatory decrease in the fraction of the day spent lying (diagrammed in Figure 8). These changes in the activity budgets increased IEC_{24} for each day (5 days of flights in late-winter, 4 days for post-calving, 3 days for the insect season).

Model estimates of ADMR and IEC_{24} in the post-calving and insect seasons (Tables 9, 10) agree with estimates from *Wildlink* data of caribou in the field (Tables 5, 6). In late winter, model estimates are higher than estimates from *Wildlink* data. This difference may be due to the record snow depth in 1991 resulting in decreased activity of the caribou in this field period.

A comparison of the effect of severity of snow depth and insect harassment on IEC_{24} for overflown minus control (IEC_{24}) animals (Table 11) shows that the effects of overflights for post-calving caribou are exacerbated in a deep snow year. A 26% increase in post-calving IEC_{24} in a deep-snow year contrasts with a 35% and 3% decreases in IEC_{24} for the late winter and insect seasons. This pattern follows the relative distribution of activity cycles between the "good" and "bad" scenarios (Tables 9, 10). The value of IEC is dependent on the daily activity budget, jet overflights, therefore, are predicted to have an increased influence when the level of animal activity is higher. A three-fold increase in the fractional change in ADMR due to overflights is seen in "bad" versus "good" years for post-calving exposed animals (Tables 9, 10). This data set is small compared with the complete overflight set, but it shows the way in which model output is affected by an environment-disturbance interaction.

Table 11. Effect of environmental variables on the difference in incremental energy cost (IEC_{24}) \pm SEM of control caribou as determined by the caribou energetics simulation model, CARIBOU.

Season	Normal	Snow + insect	P	N
Late winter	0.036 ± 0.0029	0.023 ± 0.0037	<0.001	5
Post calving	0.033 ± 0.0017	0.042 ± 0.0021	<0.001	3

Normal, refers to CARIBOU default variables for an average snow and insect season; Snow + insect, default value for deep snow winter and above average level of insect harassment.

Effects of simulated overflights on both female body weight and body fat at mid-rut (October 15) were negligible (Table 12). Females were predicted to be much lighter and thinner in the bad year scenario (Table 11). For these examples, the probability of pregnancy was not lowered from those for non-overflown control animals, but simulations in the bad year (~47% probability of conception) indicate females would not conceive.

Table 12. Simulated effects of low-altitude jet overflights on fecundity in caribou. Caribou simulations were for 3 caribou representing 3 study periods compared with the default settings of the model representing a non-overflown control animal in normal and bad year simulations. Body weight and condition estimates of the 3 cow/calf pairs and probability of pregnancy were simulated for mid-rut, October 15 (day 288). Sound exposure and predicted changes in the activity budget and energetics used to drive these simulations are shown in Tables 9 and 10.

Season, Treatment	Female		Calf	Pregnancy rate (%)
	Body weight (kg)	Fat (kg)	Body weight (kg)	
Normal year				
Control	76.1	6.51	63.0	70.2
Late-winter	76.0	6.49	63.0	70.0
Post-calving	76.0	6.50	63.0	70.0
Insect	76.0	6.48	63.0	69.9
High snow + insects				
Control	65.2	3.59	63.0	47.7
Late-winter	65.1	3.55	63.0	47.4
Post-calving	65.1	3.56	63.0	47.5
Insect	65.0	3.53	63.0	47.3

High snow + insects, represent data for a higher average winter snowfall and higher insect abundance than a normal year.

Modeling the Response of Caribou to Seasonally Repeated Noise Exposure

The possibility existed that the same animal was recaptured for collaring in the post-calving and insect seasons. The effects of noise exposure for such an animal were simulated by building an input file for CARIBOU that contained the data from a given collar from each of the three field seasons. Three radio frequencies (MHZ, 150.425, 150.565 and 151.300) were chosen for this analysis for which non-zero sound exposure levels were consistently measured. The outcome of the simulation for a control animal and 3 model animals for either a good or poor year default variables are shown in Table 13. Indices of body condition are predicted to decline marginally for either the good or poor year, reducing pregnancy rate very slightly. For the poor year simulation, pregnancy rate was below 50%, meaning the female would not conceive.

Table 13. Simulated cumulative effect of low-altitude jet overflights in late winter, post-calving and insect seasons on pregnancy rate in caribou. Tabulated body condition (weight, kg) and probability of pregnancy (%) were predicted by the computer model CARIBOU for non-overflown (control) and when noise disturbance was simulated under both good and poor environmental conditions.

Collar	Good year			Poor Year		
	Body wt.	Fat wt.	Pregnancy Probability	Body wt.	Fat wt.	Pregnancy Probability
Control	76.1	6.51	70.2	65.2	3.59	47.7
150.425	75.8	6.43	69.6	64.7	3.45	46.6
150.565	75.8	6.44	69.7	64.7	3.47	46.8
151.300	75.9	6.45	69.7	64.8	3.48	46.8
Mean	75.8	6.44	69.7	64.7	3.46	46.8

Radio frequencies of caribou collars used to collect activity counts to drive the model CARIBOU (see Table 12).

Modeling the Response of Caribou to Prescribed Noise Exposure

Field results from the post-calving data set indicate that an LT of 80 dBA was near the upper limit of sound exposures experienced by treatment caribou. This value therefore was chosen for the

following analysis. Hypothetical scenarios were run in which the effect of jet overflights started on Julian day 170 for up to 40 consecutive days, simulated under both good and poor environmental conditions.

Lower pregnancy rates were noted in poor years because caribou carry less fat under poor year scenarios. As the number of days with overflights was increased, a consistent trend to reduced pregnancy rate was observed in both scenarios due to reduced fat at the time of rut. The limiting cases of 0 and 40 days of overflights are shown in Figure 10. From Table 14, the difference in fat weight between 0 and 40 days of overflights under good environmental conditions is 6.51-6.11 (0.4) kg, which translates to a 3% absolute reduction in pregnancy rate. Under poor conditions, a 0.64 kg fat reduction is associated with a 5% reduction in pregnancy rate.

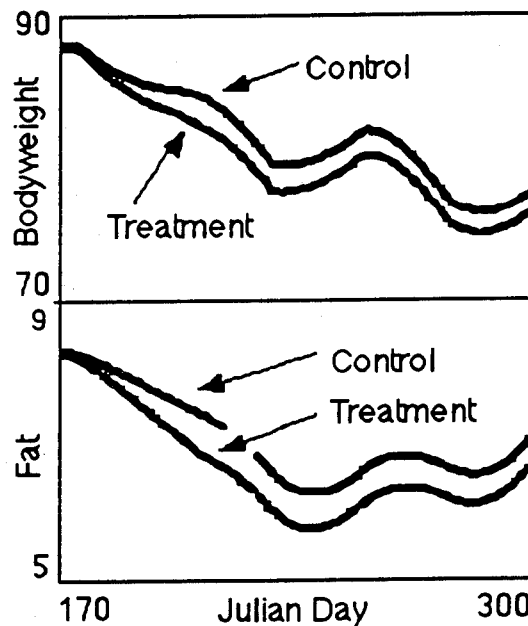


Figure 10. Time course of body and fat weights (kg) of a caribou overflown for 40 consecutive days ($L_T = 80$ dBA) beginning Julian day 170 under good environmental conditions.

Table 14. Simulated effect of consecutive low-altitude jet overflights on caribou fecundity. A single noise disturbance commenced on Julian day 170 and simulations using the model CARIBOU predicted body condition (kg) and pregnancy probability (%) for both good and poor environmental conditions.

No. of Consecutive Overflights	Good year			Poor Year		
	Body wt.	Fat wt.	Pregnancy Probability	Body wt.	Fat wt.	Pregnancy Probability
0	76.1	6.51	70.2	65.2	3.59	47.7
5	76.0	6.48	70.0	65.1	3.55	47.5
10	75.9	6.45	69.8	64.9	3.52	47.2
15	75.7	6.41	69.5	64.7	3.46	46.7
20	75.5	6.35	69.0	64.4	3.37	46.0
25	73.3	6.30	68.7	64.1	3.30	45.5
30	75.1	6.25	68.3	63.8	3.21	44.7
35	74.9	6.18	67.9	63.3	3.09	43.8
40	74.6	6.11	67.4	62.8	2.95	42.7

The algorithm adopted in CARIBOU adds time to the fraction of the day spent foraging, as was shown in Figure 8. The depression in body and fat weights as shown in Figure 10 makes it clear that the caribou did not gain adequate additional energy to fully compensate for the increase in energy expenditure associated with the noise disturbance. This is reflected in the fall fat weights (Table 14) and consequently in the probability of pregnancy, which is shown for both good and bad environmental conditions in Figure 11.

Pregnancy rate decreases with increase in noise disturbance more acutely under poor-day than good-day scenarios, indicating an interaction between sound exposure and environment. The interaction is expressed as the difference in pregnancy rates (good minus bad) against increased days of overflights in Figure 12. In effect, CARIBOU predicts that an environmentally stressed caribou will be more sensitive to the effects of noise disturbance. The particular values shown in Table 14 reflect the arbitrary choice of L_T equal to 80 dBA and 40 d of simulations.

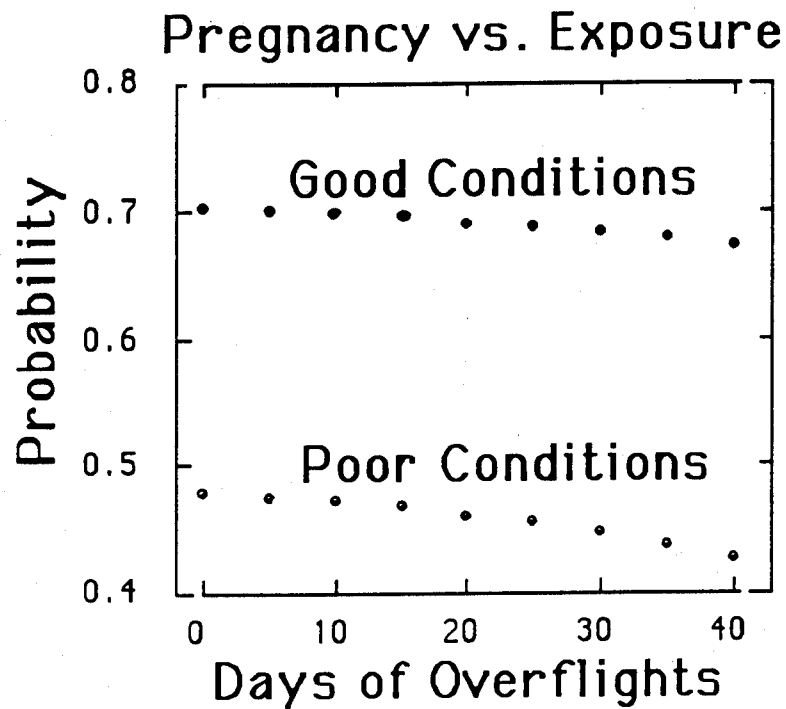


Figure 11. Pregnancy rate of caribou in relation to increasing sound exposure under good- or poor-year scenarios. Overflight days beginning on Julian day 170, the start of the insect season..

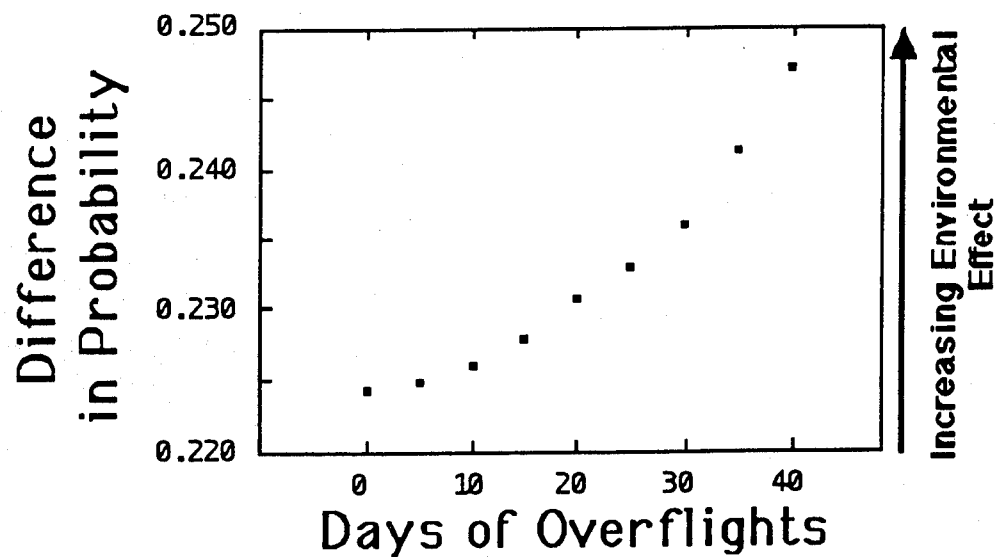


Figure 12. Interaction between pregnancy rate and environmental quality (good and bad year) with increasing consecutive overflights. The interaction is expressed as the difference in pregnancy rates with overflights beginning on Julian day 170, the start of the insect season.

Substitution of Activity for Foraging Time in Response to Noise Exposure

We simulated the effect of not allowing caribou to make compensatory feeding in response to noise exposure. A decreasing in lying time was added to active (walking and running) with no increase in foraging as described previously (Figure 8). With overflights that result in reduced foraging time, ADMR and IEC increase to a greater extent than control values. Only in the post-calving period is this latter effect more pronounced under bad conditions. Reducing foraging time in the model results in a shift towards a negative energy balance, however, the net effect on pregnancy rate is very small, the maximum decrease was 0.3 % .

DISCUSSION

Measuring responses to disturbance using HR is a well documented technique (MacArthur *et al.* 1979, 1982; Renecker and Hudson 1983; Geist *et al.* 1985; Harlow *et al.* 1987; Workman *et al.* 1992a,b,c; Chabot 1993; Krausman *et al.* 1993a,b). Purportedly, HR can give an indication of the instantaneous reaction of an animal to a disturbance and of chronic impacts if HR is elevated for extended periods. In previous studies at LARS, Fancy and White (1986) and Floyd (1987) have shown the importance of using animals sufficiently tame that they do not respond to stress of handling to determine the oxygen pulse or energy relation to HR. In this study, a change in animal position (i.e., from head down to head up) was accompanied by an increase in HR of 3 to 5 beats/min, equivalent to an O₂ consumption of 48-100 ml/min, (i.e., a 10% increase in resting metabolism; Fancy and White 1986). Chabot (1993) documented similar responses in wapiti (*Cervus elaphus*). Based on these findings we rejected the hypothesis that HR did not change with activity. Previous studies (Floyd 1987) show that an average startle response, similar to those in Figure 2, are 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 a disturbance. These are the types of responses observed when caribou were overflowed by jets (Murphy *et al.* 1993) and the utility of using HR as an adjunct to field studies is clear.

The mountainous terrain in our study area and the vast daily distances traveled by caribou made use of HR impossible for field studies. However, a laboratory study was made to highlight the potential of quantifying behavioral responses in an energy currency, in order to assess the instantaneous cost to caribou responding to low flying jet aircraft. Given the low energy costs of observable behavioral responses, our assessment is that the instantaneous energy cost is minimal; it would not measurably increase the daily energy expenditure even if animals were overflowed repeatedly. This assessment of caribou response agrees with assessments based on instantaneous HR responses of overflowed captive desert mule deer (*Odocoileus heimonus crooki*) and mountain

sheep (*Ovis canadensis mexicana*) fitted with Stuart implanted HR monitors (Krausman *et al.* 1993a). In these latter studies, simulated overflight giving a sound dose of 92 to 112 dBA significantly increased HR, which returned to normal within 2 minutes. These quantitative findings support reports for sheep (Workman *et al.* 1992b, c).

We next tested hypotheses that longer-term (i.e., daily) responses to low flying jet overflights, as evaluated by us (Murphy *et al.* 1993) may result in a significant energy cost. To do this we used activity counts (AC) to generate two energy currencies, namely the mean IEC₂₄ and ADMR. Our results show a close relation between HR and AC ($p = 0.002$; Table 3). 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), the data on concordance and correlation of HR with IEC support a strong basis for extrapolation of AC to IEC under field conditions. When all laboratory data sets were analyzed, 60 min was preferred because estimation of daily energy expenditure was more accurate (Figure 4) and data acquisition (i.e., collection of 36 units in binary code) was more easily handled. The *Wildlink* system also enabled simultaneous collection of data on multiple animals and, for the first time, we documented group synchrony of activity in caribou over 24 hours (Figure 6). Further, AC also is closely related to the ADMR of caribou ($p = 0.0001$), which enabled us to determine actual daily energetic costs of caribou responding to jet aircraft overflights.

Long-term (i.e., non-instantaneous) effects resulting from disturbance are both direct, due to the energetic-nutritional consequences of movement (White *et al.* 1976; Bleich *et al.* 1990; Harrington and Veitch 1992) and indirect due to changes in habitat use (Smith and Cameron 1985, 1991; Dau and Cameron 1986; Bleich *et al.* 1990). Our energy cost analysis shows that both energy currencies responded linearly to the dose of sound, with significance in the post-calving period (Table 7). Post-calving caribou also responded to jets by increased daily movement and activity (Murphy *et al.* 1993). We calculated that these overt behavioral responses were associated with a

4.3% increase in IEC_{24} ($P < 0.03$), and a small 2.6% ($P < 0.04$) increase in ADMR, compared with control animals. Such small increases in energy expenditure are difficult to measure directly (e.g., by isotope techniques, Fancy *et al.* 1986) and are of low physiological significance. Under good grazing conditions, one might expect caribou to compensate for such increased costs by foraging more. However, in some years summer forage can limit caribou productivity (White *et al.* 1981; Truddell and White 1981; Russell *et al.* 1993) and the movement of caribou to non-preferred habitats may be associated with multiplicative effects on productivity (White 1983) that are difficult to measure. Thus, although the direct energetic effects of jet aircraft disturbance was small in these studies, the indirect effects remain unmeasured.

Computer simulation of the daily responses of caribou to jet overflights allows testing of theoretical consequences. We first tested the predictability of the model CARIBOU by comparing its projected estimates of IEC_{24} and ADMR with our empirical estimates. 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 ($\text{kJ/kg}^{0.75}$) for control animals averaged 786, 1012, and 1009, respectively, during these 3 sampling periods (Table 6). Seasonal differences in activity patterns have been well documented for caribou (Russell *et al.* 1993) and underlie seasonal differences in energy expenditure. CARIBOU predicted seasonal differences in ADMR, but the values for ADMR were higher in late winter than was estimated by our study. For post-calving caribou, and those in the insect season, ADMR values predicted by the CARIBOU model were slightly lower but essentially agreed with our AC derived values. Differences between our estimates of ADMR in late winter and those predicted by CARIBOU may be due to the record snow depth experienced by the Delta Caribou Herd (DCH) in winter 1991, the simulated values being more realistic than extrapolations from tame caribou at LARS. 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 in energy metabolism and nutrition (e.g., appetite and heat increment of feeding, lowered resting metabolic rate). Because of these

natural seasonal differences, it is important to evaluate responses to disturbance on a seasonal basis to identify potentially sensitive times of the year. For example, in late winter, caribou did not exhibit changes in the incremental cost of activities ($p = 0.73$) or in ADMR ($p = 0.59$) in response to low-altitude jet aircraft overflights. However, post-calving there was a significant linear increase in both IEC_{24} ($p = 0.08$) and ADMR ($p = 0.06$) in treatment caribou. There also was no associated increase in IEC_{24} ($p = 0.45$) and ADMR ($p = 0.44$) in disturbed caribou during the insect harassment season.

DCH has been described as "the most highly disturbed herd in Alaska" (Davis *et al.* 1985). Low level flight training of USAF A-10, F-15, and F-16 jets of Eielson A. F. B., Alaska, occurs within the range of the DCH, a military bombing range borders the calving grounds. Although Harrington and Veitch (1992) found that calf survival was compromised by the frequency of low-altitude jet aircraft overflights 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. Our study showed a significant increase in energy expenditure in response to disturbance by military aircraft in post-calving caribou and supports concerns expressed by Harrington and Veitch (1992) even for this highly conditioned herd. Whether this disturbance can lead to an overall decrease in herd productivity is not answered by this study. The model shows that the general outcome of a set of overflight scenarios depends on habitat quality, the possibility of an interaction between habitat quality and disturbance on fecundity should be considered in developing management plans. Because fecundity is lower in "bad" than "good" years, management of overflight schedules should be reconsidered in years during, and following, heavy snow-fall and in hot-dry summers, i.e., "bad" year habitat characteristics (Russell 1991).

Ultimately the value of CARIBOU is to predict the consequences of noise disturbance on fecundity. This process was initiated in the current analysis by modeling a hypothetical scenario of consecutive jet aircraft overflights. Post-calving caribou are emerging from a winter diet, they

have limited fat reserves and are undergoing peak lactation. In general, total body weight and fat weight cannot increase, and when this is coupled with mid-summer insect harassment, recovery of body condition may not be initiated before late summer. For these reasons, the effects of disturbance may be biologically significant during the post-calving period.

CONCLUSION AND IMPLICATION FOR MANAGEMENT

Jet overflights in late-winter were associated with no change in the incremental cost of activities and the ADMR. Post-calving caribou exhibited a significant, linear increase in both IEC and ADMR with maximum daily sound exposure and the mean sound exposure. In the insect season, caribou appeared to expend no extra energy in response to low-flying jet aircraft. Extrapolation of these energetic responses to likely effects on fecundity using computer simulation showed no significant lowering of the probability of conception. If female caribou of these simulations are representative of all caribou overflown in this study, then we suggest that the energetic responses associated with changes in the daily activity budget, are likely not to affect herd productivity.

Left unstudied are the indirect effects of disturbance by low flying jet aircraft. These effects are due to using different habitats and can be expressed through population regulatory factors operating through nutrition and stochastic effects as well as differences in predation rate. Indirect effects of overflights can be modeled by CARIBOU, but the full analysis also warrants further field study.

We made no attempt to exercise the model to determine when and under what condition caribou would be most vulnerable to overflights. Nor did we attempt to determine seasonal "thresholds" of noise exposure that would result in a significant decline in individual fecundity. These effects warrant analysis and the simulation program produced for this study can be used to make such assessments. The confidence placed on such a gaming exercise can be judged by the simulated output relation of variables compared to those reported for this herd. Our validation of CARIBOU was based on *Wildlink* activity data sets for non-overflown animals. CARIBOU simulations agreed closely with these outputs. The true value of the model in its present form is to test scenarios, challenge intuition, educate those associated with management responsibility and explain likely effects to aircrews associated with making jet overflights of caribou.

A recommendation resulting from our work is that early post-calving caribou should not be subjected to repeated low-altitude jet overflights until further research shows the significant movement and behavioral effects shown by Murphy *et al.* (1993) and to energetic effects shown in this study do not carry with them a serious indirect effect on fecundity and calf growth and survival.

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APPENDIX

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ENERGETIC COSTS OF LOW-LEVEL JET AIRCRAFT OVERFLIGHT IN CARIBOU

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Energetic costs can be deduced by determining costs of observed behavioral responses, particularly when heart rate is used as an indirect measure of energy expenditure (Fancy and White, Rangifer, 1986). This project will involve simultaneous recording of heart rate and behavioral responses during low-level jet overflights. Individual caribou calibrated for both heart rate and energy expenditure will be fitted with a sound monitor system. A dose response curve relating energy expenditure to sound exposure will be developed for application to field studies and computer simulation modeling. Response to sound occurs over short time periods necessitating instantaneous measurement of heart rate and oxygen consumption. The latter requires use of an enhancement for distortion correction in the calorimetry system (Kokjer et al., J. Wildl. Manage., 1990). Initial results suggest that accurate estimates of the energy cost of the alert response and short-term activity events must be determined using this application. Research is supported by the U.S.A.F. through a cooperative agreement with the U.S.F.W.S. and the Institute of Arctic Biology.

ESTIMATING ENERGY EXPENDITURE OF CARIBOU USING PROGRAMMABLE RADIO COLLARS: POTENTIAL FOR USE IN DISTURBANCE STUDIES

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Estimation of daily activity of animals by the use of mercury tilt switches in traditional radio collars (e.g. Green & Bear 1990, *J. Wildl. Man.* 54:272-279) and satellite collars (Fancy et al. 1988, USFWS Publ 172; Klein & Bay 1990, *Hol. Ecol.* 13:269-280) is widely accepted. New radio collar technology has been introduced by Wildlink Inc. (Mech et al. 1990, *J. Wildl. Man.* 54:297-299). The Wildlink Data Acquisition and Recapture System is a programmable radio recapture collar which records mercury tilt switch activity counts (AC) in each of 24 intervals of equal length. Intervals may be from 10 to 90 min and are preset by the investigator. A triggering transmitter enables remote programming of interval length and downloading of data. We are investigating the potential of using this collar to give short time-step indices of energy expenditure (EE) in caribou. Methodology includes relating the Wildlink AC, summed over 30 min, to 1) heart rate (HR) collected simultaneously with subcutaneously implanted HR transmitters (Stuart Enterprises, Inc.) and 2) a 30 min energy expenditure index (EEI) developed by Fancy (1986: PhD thesis, UAF). The EEI is based on focal-animal, continuous monitoring, sampling technique (Altmann 1974, *Behavior* 49:227-265) which will be performed on instrumented caribou at the Large Animal Research Station (to calibrate the system) and in the field. Fancy & White (1986, *Rangifer* 1:123-130) described a linear relationship between HR, EE, and activity. In our work we have found a close relationship between HR and EE and between Wildlink AC, HR, and EEI. A 30 min interval can be used to determine periods of rest and of high activity in caribou. The objective is to use Wildlink collars to determine both daily EE and short-term energetic responses of caribou to low flying military jet aircraft. We are currently investigating the potential use of short time steps (< 30 min) to predict the EE of anthropogenic and predator-evoked flight reactions of caribou. Funded by the U.S.A.F., N.S.B.I.T. program.

Expanded abstract

Predicting energy expenditure of caribou using activity counts: potential use in disturbance studies

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Rangifer, 13 (2): 117-119

Estimation of daily activity of animals using mercury tilt switches in traditional radio-collars and satellite collars is widely accepted. In northern latitudes scientists rely almost exclusively on the use of radio-collars to gather data on caribou (*Rangifer tarandus*) (Pank *et al.* 1985; Fancy *et al.* 1990; Fancy & Whitten, 1990), muskoxen (*Ovibus moschatus*) (Reynolds, 1989; Klein & Bay 1990), and polar bears (*Ursus maritimus*) (Messier *et al.* 1992) during winter. There are disadvantages in using standard and satellite telemetry to acquire activity data, however. Standard radio-collars must be monitored continuously and activity estimated from changes in pulse rate and are useful only to differentiate between degrees of activity (Garshelis *et al.* 1982; Gillingham & Bunnell 1985). Satellite collars transmit activity data to satellites when those satellites are overhead, a limited portion of the day (Fancy *et al.* 1988; Harris *et al.* 1990). Also, satellite collars can only discriminate between two levels of activity and data cannot be stored (Fancy *et al.* 1988).

A programmable radio collar introduced by Wildlink Inc. (MN) records mercury tilt switch counts (AC) in each of 36 intervals of equal

length (Note: the collars have since been upgraded and have a year of memory and battery life). A triggering transmitter enables remote programming of interval length and downloading of data (Kunkel *et al.* 1991; Mech *et al.* 1990). Counts collected in an interval correspond to the activity that took place in that interval (e.g. low counts, low levels of activity). Our objectives were to 1) calibrate the Wildlink activity counter for caribou, 2) test the Wildlink radio-collar for use in investigating the effects of low-level jet aircraft overflights on caribou.

We conducted 26 h behavioral observations on captive caribou fitted with Wildlink radio-collars at the University of Alaska Fairbanks Large Animal Research Station (LARS). Daily activity budgets were determined from observations and from Wildlink AC. We related Wildlink AC to 1) heart rate (HR) collected simultaneously using subcutaneously implanted HR transmitters (J. Stuart Enterprises) and 2) an energy expenditure (EE) index developed by Fancy & White (1986; Table 1). HR and EE are summed over time using the time interval set for AC (Fig. 1). We investigated the potential

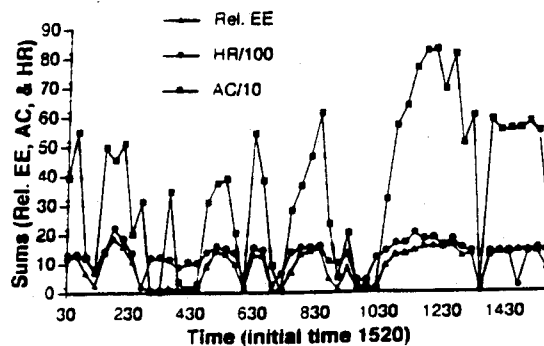


Fig. 1. The relationship between rel. EE, HR, and AC through time.

of using this collar to give short time-step, quantitative indices of EE in caribou and have developed a prediction equation estimating EE from AC (Fig. 2):

$$Y = 0.02X + 2.08$$

There was a significant amount of variation between animals in terms of counts/activity but patterns were similar (Fig. 2). Overall, 30 and 60 min intervals accurately predicted rest/activity cycles in caribou whereas a 60 min interval accurately predicts both interval and daily EE. As the AC interval length increases the ability to predict *relative* EE from AC increases as well (Fig. 3). However, resolution may be decreased. A shorter interval (1 to 10 min) may be needed to detect short-term responses to acute disturbance. Head movement during a lying bout elevates AC resulting in decreased predictability of EE (i.e. relatively high counts during a period of low activity). Similar problems have been documented when using standard radio telemetry (Gillingham & Bunnell, 1985).

Kunkel *et al.* (1990) found that the Wildlink activity monitoring system may be used to re-

liably achieve estimates of energy budgets. The use of Wildlink AC for monitoring caribou activity and response to disturbance is also promising. The Wildlink radio-collar is sensitive enough to detect severe response (i.e. abnormally high peak of activity) to an acute disturbance or a long-term response (i.e. resulting in a phase-shift of the daily cycles) to chronic disturbance. Therefore, we believe that the collar will be particularly useful when comparing disturbed to undisturbed caribou. This technique will also be useful when comparing activity cycles of disturbed caribou before and after disturbance.

A 60 min interval is most useful for predicting *relative* EE. The relationship between *relative* EE and AC may not be linear, however. Figure 3 shows as AC increases, EE levels off. This may be due to the animal reaching a maximum level of EE for a given period of time (30 or 60 min) and, also, to the sensitivity of the mercury tilt switch. AC's are collected with virtually every head movement, regardless of whether the animal is lying, standing, walking or running. As a result, AC may be relatively high during periods of low, moderate, or high EE. More analyses using nonlinear regression are planned to further investigate the potential of shorter intervals which may be useful in discerning less severe reactions to disturbance.

Table 1. Incremental costs of activities over resting metabolic weight (RMR; Fancy & 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

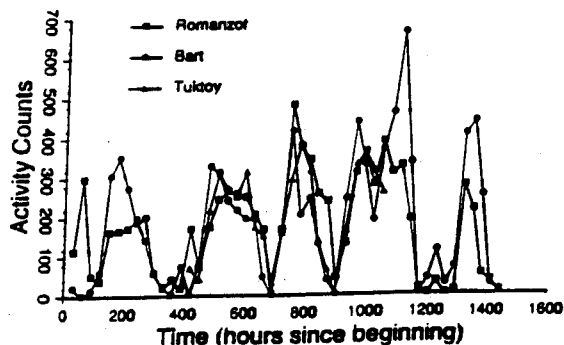


Fig. 2. Three male caribou cycle together during a 24 h behavioral watch. However, there is variability in activity counts between animals.

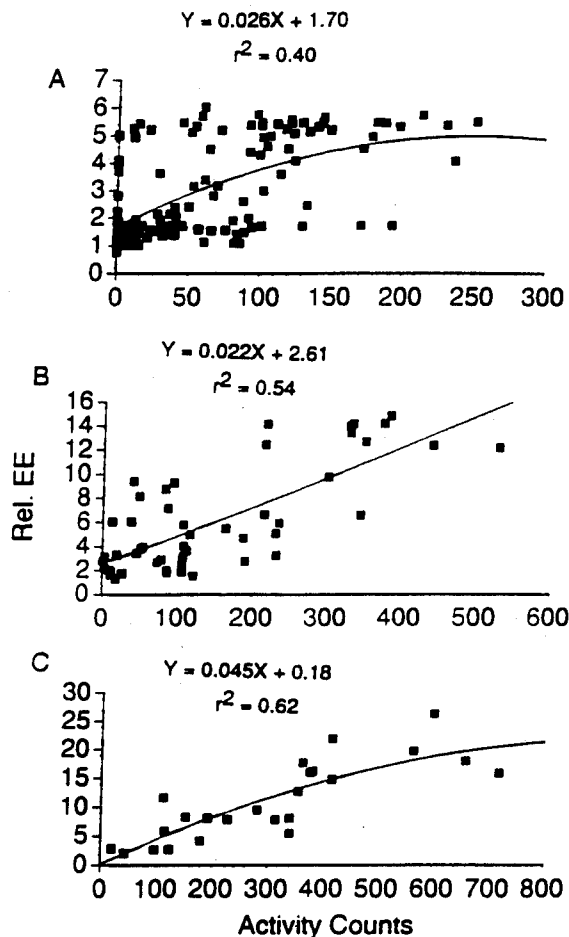


Fig. 3. As interval length increases predictive capability improves. A) 10 min, B) 30 min, and C) 60 min interval length using data from 17 July 1991.

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Karen Higgs was available and willing to help with animal handling and organization of behavioral watches. Other employees of LARS conducted observations including Kim DeRuyter and Sandy Kennedy. Bill Hauer provided animals, equipment, and computer expertise. A number of students were enthusiastic and volunteered their time to observe caribou on many occasions and at many late hours. Particularly helpful were Valerie Baxter, Mike Smith, Ian White, Jon Bishop, Damon Bender, Margot Monhollen and Todd Dwyer. This study was funded by the U.S.A.F., N.S.B.I.T. program.

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EFFECTS OF OVERFLIGHTS ON MOVEMENTS AND ACTIVITY OF CARIBOU

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We investigated the effects of low-level jet aircraft overflights on female caribou of the Delta Herd in 1991. Two groups of 5 caribou (one a treatment and one a control group) were outfitted with Wildlink, Inc. radio collars in each of 3 seasons: late winter (March/April), post-calving (early June), and insect harassment season (July/August).

The two groups were ≥ 10 miles apart at the time of collaring. Treatment caribou were also outfitted with Animal Noise Monitors (ANM's) which recorded and stored all sound equivalent levels (SEL's) above an exposure of 85 dB, and were subjected to low-altitude jet aircraft overflights by U.S.A.F. A-10, F-15, and F-16 aircraft. All animals had calves at side at the time of capture in June and July. We determined distance moved from daily relocations and compared daily movements of treatment versus control animals on ranked daily distance moved by season. Daily activity was determined using a mercury tip-switch and total counts per day were analyzed within each animal using analysis of variance across days (comparing treatment and control days within an animal). There were no significant differences in daily distance moved (km) between treatment and control animals in April and July. Treatment animals moved significantly further (7.8 ± 1.27 km) than control animals (5.2 ± 1.15 km) in June. Further, activity levels were similar on treatment and control days for all animals in April and July whereas treatment animals were significantly more active on treatment days than on control days in June. Our findings suggest an increased level of sensitivity by immediately post-calving females to disturbance by jet aircraft. Funding for this project was provided by the U.S.A.F., N.S.B.I.T. program.

ENERGETIC CONSEQUENCES OF LOW ALTITUDE JET AIRCRAFT OVERFLIGHTS ON CARIBOU

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We investigated the effects of low-altitude jet aircraft overflights on female caribou of the Delta Herd in 1991. Two groups of 5 caribou (one a treatment and one a control group) were outfitted with Wildlink, Inc. radio collars in each of 3 study periods: late winter (March/April), post-calving (early June), and insect harassment season (July/August). The two groups were ≥ 10 miles apart at the time of collaring. Treatment caribou were also outfitted with Animal Noise Monitors (ANM's) which recorded and stored all sound equivalent levels (SEL'S) above an exposure of 85 dBA, and were subjected to low-altitude jet aircraft overflights by USAF A-10, F-15, and F-16 aircraft. Daily activity was determined using a mercury tip-switch. The pattern of energy expenditure was determined using equations derived from research using captive caribou at the Large Animal Research Station (LARS), Institute of Arctic Biology. Daily, energy expenditure estimates were analyzed within each treatment animal using analysis of variance across days (contrasting days with and without overflights). We also compared daily energy expenditure of control and treatment animals. Overflights increased energetically costly activities, particularly in early post-calving. Funding for this project was provided by the USAF, NSBIT program.

EFFECTS OF LOW-ALTITUDE JET AIRCRAFT OVERFLIGHTS ON ACTIVITY AND AVERAGE DAILY METABOLIC RATE OF CARIBOU

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Military training exercises have increased in Alaska in recent years and the effects of low-altitude training on wildlife resources, such as caribou (*Rangifer tarandus granti*), have caused concern among northern residents and resource agencies. We investigated the effects of low-altitude jet aircraft overflights on female caribou of the Delta Herd in 1991. Two groups of 5 caribou (one a treatment and one a control group) were outfitted with Wildlink, Inc. radio collars in each of 3 study periods: late winter (March/April), post-calving (June), and insect harassment season (July/August). Treatment caribou were also outfitted with Animal Noise Monitors (ANM's) which recorded and stored all sound equivalent levels (SEL's) above an exposure of 85 dBA, and were subjected to low-altitude jet aircraft overflights by U.S.A.F. A-10, F-15, and F-16 aircraft. Daily activity was determined using a mercury tip-switch. The pattern of energy expenditure was derived from equations developed using captive caribou at the Large Animal Research Station, Institute of Arctic Biology. Average Daily Metabolic Rate (ADMR) was estimated using these equations and analyzed using analysis of variance, comparing days with overflights and days without overflights for treatment and control animals. The number of resting and active bouts per day, the mean length of resting and active bouts, daily time spent resting and active, and the daily distance moved were each analyzed also using ANOVA. Caribou subjected to low-altitude jet aircraft overflights increased energetically costly activities and thus, ADMR, particularly in early post-calving. These caribou also traveled farther than their undisturbed counterparts during post-calving. Funding for this project was provided by the U. S. Air Force, N.S.B.I.T. program.

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Modeling energy and reproductive costs in caribou exposed to low flying military jet aircraft.

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We used simulation modeling to evaluate the effects of low-altitude military jet aircraft on the productivity of caribou. The base model (CARIBOU, CWS Whitehorse, Yukon Territory) uses daily intake and expenditure of energy to assess the condition of female caribou throughout the annual cycle. We added a subroutine that accounted for the influence of overflights on energy balance to predict the likelihood of conception. Caribou responses to overflights were evaluated by equipping free-ranging caribou with radio collars and activity sensors that could distinguish between resting and active periods. Collared animals were exposed to 110 overflights by A-10, F-15, and F-16 jet aircraft during late-winter, post-calving, and the insect season. Noise exposure levels for individual animals either were measured directly with collar-mounted dosimeters or were estimated based on the proximity of the caribou to the aircraft during the overflight. A Time-averaged Sound Level (L_T) was calculated from the total daily noise exposure for each animal and multiple regression was used to evaluate the influence of daily noise exposure on daily hours spent resting. Results of these analyses then were used to modify the time budgets in the CARIBOU model. That is, if time spent resting declined, then time spent in the two classes (lying and standing) were proportionally redistributed into the three active classes (foraging, walking, and running). Model simulations indicated that caribou increased forage intake in response to increased noise exposure, but it also predicted that increased exposure would cause a reduced accumulation of body fat. Because body fat in fall has successfully been used to predict the probability of pregnancy (see Gerhart et al., 1993), this relationship was used in the model. Preliminary model simulations indicate that increased noise exposure decreases the probability of pregnancy and that unfavorable environmental conditions (e.g., deep snow and severe insect harassment) exacerbate the situation. The threshold at which point the caribou fail to conceive has not been determined at this time, but appears to be well beyond the exposure to aircraft that caribou in the Delta herd are currently experiencing.

SEASONAL CHANGES IN ACTIVITY CYCLES OF CARIBOU

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Activity patterns of ruminants are driven by seasonal time available for feeding and hence photoperiod, plus components of feeding dynamics that balance maximizing grazing time with forage digestion. This system has predictable outcomes for activity patterns based on ecological and nutritional factors. Our objective was to determine typical seasonal activity patterns of captive caribou (*Rangifer tarandus*) given *ad libitum* food. Data then were compared simultaneously with free-ranging caribou of the Delta herd at the same latitude (63 ° N). We developed a remote sensing technique to measure activity patterns from activity-monitoring radio collars (*Wildlink, Inc.* ® St. Paul, Minnesota) on wild caribou. These collars were calibrated using captive caribou at the Large Animal Research Station (LARS). Published data on winter activity patterns of reindeer on the Seward Peninsula (Collins & Smith, 1989) and year-round data on caribou of the Denali herd (Boertje, 1985), both at 63 ° N, were compared to caribou of the Porcupine (Russell *et al.* 1993), and Central Arctic (White *et al.* 1975, Roby 1978) herds, located further north (68 ° N).

Cyclic, synchronous activity patterns were apparent for LARS and Delta caribou except in the insect season. Synchrony was related to activity beginning at sunrise and ending at sunset. LARS and Denali herd caribou had constant active and resting bout lengths year-round. Delta, Central Arctic, and Porcupine caribou had shorter bout lengths in summer (post-calving) than in late winter. Differences in bout length were attributed to differences in range condition rather than photoperiod. Longer bout lengths of Delta caribou in winter were attributable to low forage availability due to record deep snow. All herds, excepting LARS caribou, became asynchronous during the insect harassment season. Active bouts became significantly longer due to increased standing, trotting, and galloping in response to insects.

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