Responses of Caribou to Overflights by Low-Altitude Jet Aircraft
Author(s): Julie A. K. Maier, Stephen M. Murphy, Robert G. White and Michael D. Smith
Source: *The Journal of Wildlife Management*, Vol. 62, No. 2 (Apr., 1998), pp. 752-766
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3802352
Accessed: 05/06/2014 12:10

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Wiley and *Wildlife Society* are collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management.*

http://www.jstor.org

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

STEVENS, V., AND D. B. HOUSTON. 1989. Reliability of age determination of mountain goats. Wildlife Society Bulletin 17:72–74.

TAYLOR, I. R. 1991. Effects of nest inspections and radio-tagging on barn owl breeding success. Journal of Wildlife Management 55:312–315.

VALKENBURG, P., R. D. BOERTJE, AND J. L. DAVIS. 1983. Effects of darting and netting of caribou in Alaska. Journal of Wildlife Management 47:1233–1237.

VAN DER EEMS, K., AND R. D. BROWN. 1986. Effect of caffeine sodium benzoate, ketamine hydrochloride, and yohimbine hydrochloride on xylazine hydrochloride-induced anorexia in white-tailed deer. Journal of Wildlife Diseases 22:403–406.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WHITE, M., F. F. KNOWLTON, AND W. C. GLAZENER. 1972. Effects of dam–newborn fawn behavior on capture and mortality. Journal of Wildlife Management 36:897–906.

Received 28 June 1996.
Accepted 14 July 1997.
Associate Editor: Fairbrother.

RESPONSES OF CARIBOU TO OVERFLIGHTS BY LOW-ALTITUDE JET AIRCRAFT

JULIE A. K. MAIER,[1] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
STEPHEN M. MURPHY, ABR, P.O. Box 80410, Fairbanks, AK 99708, USA
ROBERT G. WHITE, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
MICHAEL D. SMITH, ABR, P.O. Box 80410, Fairbanks, AK 99708, USA

Abstract: Military training exercises have increased in Alaska in recent years, and the possible effects of low-altitude overflights on wildlife such as barren-ground caribou (*Rangifer tarandus*) have caused concern among northern residents and resource agencies. We evaluated the effects of overflights by low-altitude, subsonic jet aircraft by U.S. Air Force (USAF) A-10, F-15, and F-16 jets on daily activity and movements of free-ranging female caribou. This study was conducted on caribou of the Delta Caribou Herd in interior Alaska during each of 3 seasons in 1991: late winter, postcalving, and insect harassment. Noise levels experienced by caribou were measured with Animal Noise Monitors (ANMs) attached to radiocollars. Caribou subjected to overflights in late winter interrupted resting bouts and consequently engaged in a greater number of resting bouts than caribou not subjected to overflights ($P = 0.05$). Caribou subjected to overflights during postcalving were more active ($P = 0.03$) and moved farther ($P = 0.01$) than did caribou not subjected to overflights. Caribou subjected to overflights during the insect season responded by becoming more active ($P = 0.01$). Responses of caribou to aircraft were mild in late winter, intermediate in the insect season, and strongest during postcalving. We conclude that females with young exhibit the most sensitive response to aircraft disturbance. Accordingly, military training exercises should be curtailed in areas where caribou are concentrated during calving and postcalving.

JOURNAL OF WILDLIFE MANAGEMENT 62(2):752–766

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

As human populations expand into traditional wildlife habitats, evaluating the effects of human activities on wildlife populations becomes critical. In Alaska, vast tracts of uninhabited land make this state an attractive location for increasing the range and intensity of military training exercises. Military exercises have increased in Alaska in recent years by 33%, and the postulated effects of low-altitude overflights by jet aircraft on wildlife such as caribou have caused concern among northern residents and resource management agencies (Gladwin et al. 1987). In response to these concerns, the USAF initiated a number of research projects to better understand the effects of their training exercises on wildlife. Caribou were selected for this study because detailed models of their energetics are available, and the Delta Herd of interior Alaska occurs near Eielson Air Force Base, which is an area used regularly by the USAF for jet-training exercises.

[1] E-mail: ftjak@uaf.edu

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

Resource management agencies have been addressing wildlife and habitat disturbance for many years and have identified a variety of problems regarding aircraft disturbance of ungulates, including (1) movement from the area of disturbance and changes in habitat use by mountain sheep (*Ovis canadensis*; Krausman and Hervert 1983, Krausman et al. 1986, Bleich et al. 1990, 1994) and mountain goat (*Oreamnos americanus*; Côté 1996), (2) decreased foraging efficiency of desert bighorn sheep (Stockwell et al. 1991), (3) increased heart rate in mountain sheep (MacArthur et al. 1979, 1982; Krausman et al. 1993, Weisenberger et al. 1996) and desert mule deer (*Odocoileus hemionus*; Weisenberger et al. 1996), (4) panic running (Calef et al. 1976), (5) decreased frequency of nursing (Gunn et al. 1985), (6) overt behavioral responses by barren-ground caribou (Murphy et al. 1993) and woodland caribou (*R. t. caribou*; Harrington and Veitch 1991), and (7) decreased calf survival of woodland caribou (Harrington and Veitch 1992). The above studies investigated the responses of several ungulates to distinct aircraft types (i.e., fixed-wing, helicopter, jet aircraft). Ungulates respond differently to the various types of aircraft, but responses typically were strongest to helicopter overflights.

Harrington and Veitch (1992) noted that female woodland caribou exposed to low-altitude overflights by jet aircraft experienced lower survival of their calves than female caribou not subjected to this disturbance, whereas Valkenburg and Davis (1985) concluded that caribou of the Delta Herd are habituated to aircraft disturbance. Although the Delta Herd was exposed to frequent low-altitude overflights by military and civilian aircraft for a number of years (more than any herd in Alaska), Valkenburg and Davis (1985) concluded that disturbance had not adversely affected productivity, until at least 1984 (Davis et al. 1985). However, rather than by evaluation of individual response, the effects of overflights on the Delta Herd were based on comparison of annual trends in productivity of the Delta Herd to other herds in Alaska not exposed to low-altitude overflights by military aircraft.

Seasonal differences in responses to overflights may occur because seasonal differences in activity patterns have been documented for a number of caribou herds in Alaska (Roby 1978, Boertje 1985, Russell et al. 1993). Variability in seasonal activity patterns results from seasonal differences in food resources and environmental variables (e.g., snow depth, insect harassment, predation, photoperiod), the presence of neonatal calves in early summer, and breeding behavior during the rutting season. Additionally, Maier (1996) compared length of active bouts from free-ranging caribou of the Delta, Denali, and Porcupine herds, and captive caribou from the Large Animal Research Station (LARS), Institute of Arctic Biology, University of Alaska Fairbanks, and documented between-herd differences within a season (late winter and postcalving), resulting largely from nutritional constraints. Between-season differences in activity patterns of Delta Herd caribou were evident as well (Maier 1996).

Because of these natural differences in activity among seasons, we evaluated responses to disturbance on a seasonal basis to identify potentially sensitive times of the year. The goal of this research was to quantify long-term responses of caribou to overflights by subsonic jet aircraft flying at altitudes <33 m above ground level (agl). Our specific objectives were (1) measure the noise exposure experienced by caribou overflown by jet aircraft, (2) determine activity cycles and movements of caribou exposed to overflights by low-altitude jet aircraft, and (3) evaluate responses of caribou to overflights as a function of noise exposure.

STUDY AREA

Field activity occurred during 3 periods: late winter (30 Mar–6 Apr 1991), postcalving (7–16 Jun 1991), and the insect harassment season (26 Jul–3 Aug 1991). Reconnaissance surveys were flown during the week before each sampling period to locate concentrations of caribou from the Delta Herd within its 9,600-km^2 range (Davis et al. 1985). We located animals previously radiocollared by the Alaska Department of Fish and Game (ADFG) and ascertained a general impression of herd distribution. A study area and a location for our field camp then was selected based on the distribution of caribou and logistical considerations. Locations of the study areas differed among sampling periods but were always located on the north side of the central Alaska Range (64°14′N, 148°34′W; 63°35′N, 146°14′W; Fig. 1).

The range of the Delta Herd is physiographically diverse, with rugged, glaciated peaks and ridges (1,500–3,500 m elevation) to the north and the Tanana Flats (150–600 m) to the south.

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

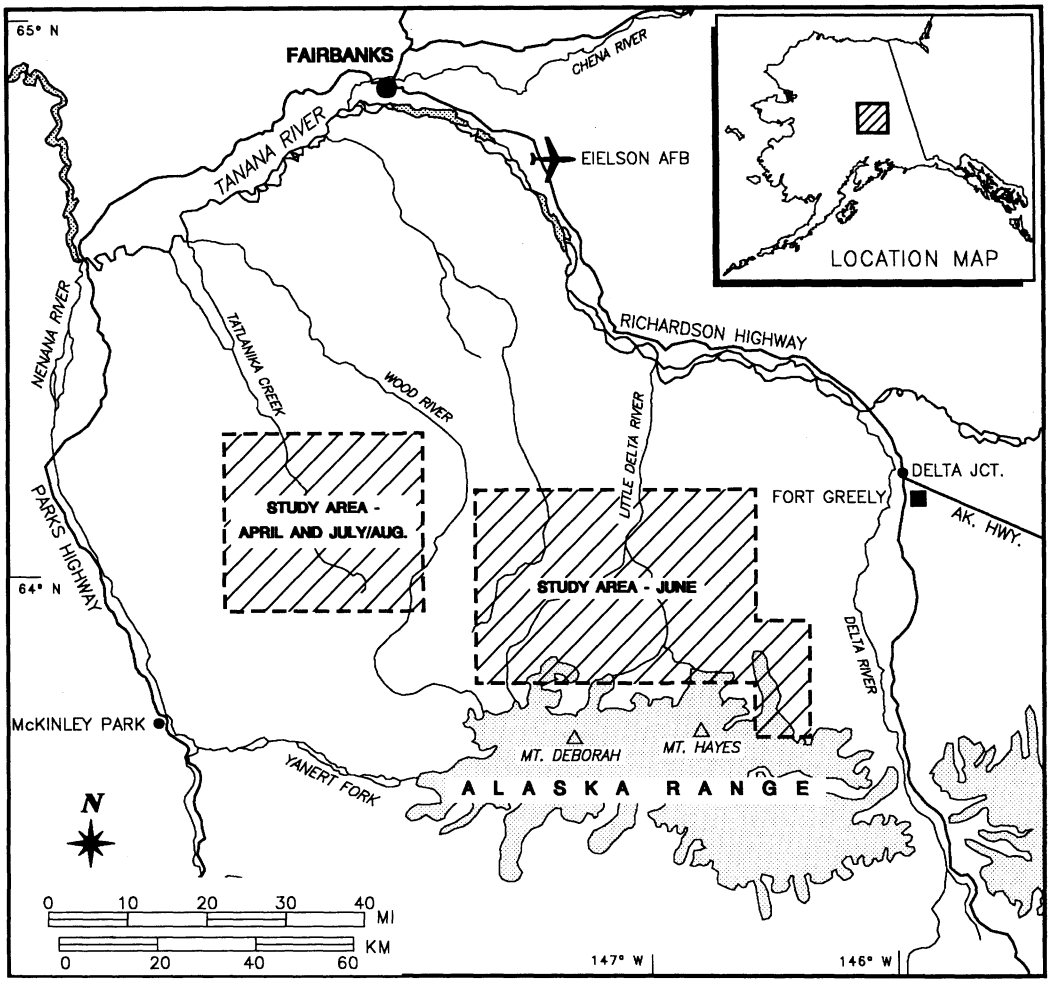

Fig. 1. Location of study areas in Alaska used to observe the effects of low-altitude overflights by military jet aircraft on caribou, 1991.

Foothills (1,000–1,500 m) rise from the Tanana Flats, and it is in the foothills that the Delta Herd spends much of its time. The foothills are dissected by northward-flowing glacial streams and steep-sided valleys. Timberline is located between 600 and 800 m; forest vegetation predominates in the Tanana Flats, and tundra dominates in the foothills. Dominant species of trees are white spruce (*Picea glauca*), black spruce (*P. mariana*), paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*; Fleischman 1990). Tundra communities are dominated by shrub birch (*Betula glandulosa*), willow (*Salix* spp.), ericaceous shrubs, sedges (*Carex* spp., *Eriophorum* sp.), mosses, and lichens (Fleischman 1990).

METHODS

We captured and instrumented caribou with radiocollars and ANMs (Murphy et al. 1993) prior to onset of each sampling period. A team of 3 scientists, using both helicopter and fixed-wing aircraft, flew to the designated study area at least 2 days before the beginning of the overflights and captured and instrumented 2 groups of up to 5 adult (≥2 yr old) female caribou by darting them from a helicopter. Darts contained a mixture of carfentanil (0.036 mg/kg body mass) and 100 mg xylazine. All animal capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks (Project 90-011).

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

One group of 5 caribou, the treatment group, was designated to be overflown by jet aircraft. We captured 5 other animals, the control group, at least 16 km from the treatment group. Control animals were not exposed to overflights. All captured animals were instrumented with Wildlink radiocollars (Wildlink, St. Paul, Minnesota, USA) equipped with VHF radio transmitters and an activity counter. We also outfitted the 5 animals in the treatment group with ANMs, which were protected by a cordura pouch with an aperture for a microphone. The pouches were affixed to the top of the collars whereby microphones would be exposed directly to the noise from aircraft. After collaring, we gave the caribou an intramuscular injection of penicillin (100 mg), a topical application of antibiotic powder, and the reversing agents naloxone (150 mg naloxone/mg carfentanil) and yohimbine (0.2 mg/kg body mass). We gave caribou ≥4 days to recover before we began data collection. A 4-day period of recovery presumably was adequate because collared caribou behaved similarly to uncollared caribou before and after the overflight period (determined from activity budgets of collared and uncollared caribou located in the same group; S. M. Murphy, unpublished data).

We began days scheduled for overflights with a radiotracking flight to locate all of the instrumented animals in the treatment group. A team of biologists and an air controller began observing 1 caribou in the treatment group that was selected based upon its availability to the observation team and accessibility by jet aircraft (e.g., animals located in box canyons were avoided). Once on site, the air controller installed the radio equipment and waited to hear from USAF pilots in the vicinity. The air controller then notified the pilots of the location of treatment caribou and directed the jets along specific flight paths as requested by biologists. In most instances, pilots were directed to fly directly over the caribou at 33 m agl and at 100% power settings. Pilots also were instructed to maintain ≥5-min intervals between multiple overflights.

Noise Exposure

We measured noise generated by jet aircraft via prototype ANMs and stationary acoustical noise monitors. Because the primary objective for noise monitoring was to measure noise exposure experienced by caribou overflown by jet aircraft, it was necessary to design equipment capable of accurately measuring noise exposure for free-ranging animals. The prototype ANMs were developed specifically for this program and represented the first time that a measurement of noise exposure was made on free-ranging animals in their natural habitats.

Because of their unique design, the ANMs permitted collection of noise exposure information over long periods of time (up to 6 months) and under a variety of environmental conditions. The ANM weighs about 450 g and is mounted on a collar that also carries a radiotransmitter used to locate the animal. Unlike most acoustical devices, the ANM can operate under a wide range of environmental conditions, including temperature variations from −28°C to 43°C. Longevity of the device is attained by keeping the unit in a semidormant state until a series of adjustable thresholds have been exceeded. Thus, battery life was optimized because only events associated with aircraft overflights were measured. The ANMs measure and calculate a number of acoustic parameters, such as a maximum noise level ($L_{maximum}$) and sound exposure level (SEL), via both A- and C-weighted scales (American National Standards Institute 1990). A-weighted SEL in decibels (dBA) was the noise descriptor selected for the analysis of the noise "dose" received by the target caribou. A-weighting represents the sensitivity of normal human hearing, and many animals have a similar hearing frequency response. The ANM memory stored the sound, date, time, and some data on activity. Each ANM was powered by 3 one-half, C-sized lithium cells for data collection and a lithium button cell for data storage. A Sennheiser Model KE 4-211-2 minicapsule microphone (Wildlife Computers, Redmond, Washington, USA) treated with a chemical waterproofing compound was used to record aircraft noise events.

Among the hazards of outdoor noise measurement is the environment, particularly the presence of wind conditions. Solutions to this problem include use of large "windscreens" to reduce the effect of wind noise under some conditions and avoiding measurements when the prevailing wind is too high. The ANMs, which are not accessible to the experimenter after deployment, incorporated both options.

During the windy late-winter sampling period, we programmed 2 ANMs with a noise-event threshold of 90 dBA, and 3 ANMs with a noise-

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

event threshold of 85 dBA. The noise threshold had to be exceeded for >2 sec for monitor activation to occur. During the insect season and postcalving period, we programmed all ANMs to record all noise events that exceeded 85 dBA for >2 sec.

There were several technical problems associated with the use of the prototype ANMs. Batteries were the primary problem, especially during the late-winter sampling period, although some units were problematic throughout the study. The ANM housing limited the size of the batteries, which discharged in cold temperatures on several occasions. Another problem inherent to the nature of the prototypes was the level of reliability of the units; some units consistently functioned well and some units consistently had problems. A secondary approach used stationary acoustical noise monitors located in the general vicinity of the experiment to record noise generated by overflights at fixed positions. We used these measurements as backups to ANM data and a means to verify the performance of the ANM under some conditions. The secondary measurement method relied on several Larson Davis Model 870 precision-integrating sound level meters (Larson Davis, Provo, Utah, USA). These meters were equipped with LD 900B microphone preamplifiers, Brüel and Kjær Model 4155 Electret microphones (Bruel and Kjaer, Budapest, Hungary), windscreens, and external 12-V batteries, and were placed in strategic locations in the study area. We attempted to locate this equipment as closely as possible to a caribou group with instrumented animals. These secondary noise measurements permitted inference of the noise exposure of animals at a fixed location. In practice, the caribou group would travel significantly between the time the instrumentation was placed and the overflights occurred, or the individual caribou fixed with ANMs would not remain in the same group but would be dispersed far away from each other. We programmed these remote, fixed-site monitors to record equivalent sound level (L_{eq}) on an hourly basis and to record single noise events >70 dBA. Single event noise measurements included $L_{maximum}$ and SEL.

The SEL is a measure of the total amount of acoustical energy generated during an event and is calculated by logarithmically integrating the magnitude of sound over the time period of that event. For each aircraft overflight, the SELs measured by the ANMs were used to describe the noise exposure of each individual or groups of caribou that contained instrumented animals. For caribou for which noise measurements from ANMs were not available, we used the OMEGA 14.6 Aircraft Noise Prediction Program developed by the USAF to estimate the SEL. Variables required to estimate SEL with this program included aircraft type, number of aircraft, flight speed, power setting, and slant range (i.e., line of sight distance) from the aircraft to the caribou. Slant ranges calculated for animals not directly observed may have been inaccurate because of differences in the time when telemetry location was fixed and when overflights occurred. The SELs were measured 58% of the time, via ANMs, across all seasons and were estimated (42% across all seasons) for each control animal and for treatment animals. In late winter, the cold weather (−34°C at night) caused the ANMs to discharge on several occasions, which resulted in battery failure in 2 of 5 units. We adjusted estimated SELs via correction factors calculated for each season and type of aircraft by averaging the difference between estimated and ANM-based measurements from caribou for which both measures were available. In addition to SEL, we calculated a time-averaged sound level (L_T) to estimate daily noise exposure for each animal via the formula

$$L_T = 10\log_{10}[1/_T \sum_{i=1}^{N} 10^{SEL_i/10}],$$

where SEL_i is the SEL of the ith event in a series of N events over the time period T (American National Standards Institute 1990). We determined both the number of overflights ≥85 dBA and ≤1 km and the loudest overflight of the day for each treatment animal for each day. We used these variables as independent variables in regression analyses.

Accuracy of the ANMs was assessed in a study of the effects of jet aircraft overflights on peregrine falcons (*Falco peregrinus*) in interior Alaska (R. J. Ritchie et al. 1996. Peregrine falcon surveys and noise monitoring in Yukon MOAs 1–4 along the Tannana River, Alaska, 1995, unpublished report. Alaska Cooperative Fish and Wildlife Research Unit, Fairbanks, Alaska, USA). Analysis of the paired event data from 4 nests indicated the average difference of SEL between ANMs varied from 0.2 dBA to

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

1.7 dBA (n = 60 aircraft overflights; B. A. Kugler. 1996. Noise exposure of peregrine falcon nests for the 1995 season: an analysis of data collected using Animal Noise Monitors (ANM), unpublished report. Krisand Consulting and Research, Encino, California, USA). The standard deviation varied between 0.7 dBA and 1.1 dBA, and both statistics showed excellent agreement of the relative noise exposure value measured.

Activity Cycles

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

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

The relation between activity counts recorded by Wildlink collars and caribou activity budgets was evaluated via captive male and female caribou at LARS. Maier (1996) documented close agreement between activity counts, energy expenditure, and observed activity of captive caribou. Equations developed from that work on captive animals were used to interpret activity counts collected on wild caribou. The concept of "resting threshold" is of specific importance to the results presented in this paper. When comparing activity counts from radiocollars to observed activity of caribou, Maier (unpublished data) noted that caribou invariably were resting when activity counts were <20% of the largest activity count for the entire 24-hr observation period, and active when counts were above this 20% threshold. The "resting threshold" must be calculated for each animal and for each observation period because of between-collar differences in activity counts. These differences in activity counts among collars may be due to slight differences in position of the mercury tip-switch or to differences in collar-fit between animals. Hence, the "resting threshold" was defined as the activity count sum above which an animal was likely to have been active and was calculated for each caribou in each observation period. We calculated the resting threshold for each wild caribou, each season, as resting threshold = 0.20 × largest hourly activity count of the season.

We screened activity counts of wild caribou via the leverage technique, whereby we removed influential points (outliers) when they had ≥2.5 times the leverage of the average point (Neter et al. 1985). We established the resting threshold to partition each 24-hr period into resting and active bouts for each of the animals equipped with Wildlink collars. Thus, we defined an active bout as the sum of consecutive 1-hr intervals during which activity counts exceeded the resting threshold. We calculated the number of resting and active bouts, the mean length of resting and active bouts, and the daily time spent resting and active each day. For comparisons of treatment and control animals, we standardized daily counts of activity to the proportion of total counts per season (i.e., daily activity counts/total counts per season) because of suspected variability between radiocollars.

We initially captured caribou in 2 disparate areas in 2 groups of 5 each, with the intention that 1 would be the treatment group, the other the control. However, due to extensive movements of caribou in both capture groups, some animals intended as control were subjected to overflights, while some intended treatment animals were not. We assigned animals to treatment or control groups after verifying that individuals had been overflown on a particular day. For example, if an animal from the proposed control group moved into the overflight zone and was exposed to overflights ≥85 dBA,

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

it was classified as a "treatment" animal for that day (this occurred 11 times, 10 during the postcalving period). Conversely, if an animal from the treatment group was not exposed to overflights on a particular day, it was classified as a "control" animal for that day (this classification occurred frequently, because there were numerous days with no overflights). Hence, sample sizes are based upon the number of control and treatment animals each day summed over the entire season rather than the initial number of captured control and treatment animals.

We analyzed activity cycles by comparing treatment and control groups and by stepwise multiple-regression analysis for treatment animals. We made comparisons between treatment and control groups for number of active and resting bouts per day, mean length of active and resting bouts, daily time spent active and resting, and proportion of total counts per season. We used analysis of variance (ANOVA) for these comparisons and assessed significance at $\alpha = 0.05$. We conducted all analyses with SAS statistical software (SAS Institute 1985).

Movements

We plotted locations of instrumented caribou and caribou under direct observation, together with the route of each overflight, on digitized study area maps via Atlas Geographical Information System (GIS) software. We did not assess error associated with flight paths but surmised it to be constant and unbiased. We performed spatial analyses to determine the slant range from each instrumented caribou to each aircraft and the distance traveled between daily locations for each animal. We calculated the minimum distance traveled by each caribou between 2 successive locations recorded at 24-hr intervals by connecting locations with straight lines.

We used 1-way ANOVA to compare daily distance traveled between treatment and control animals, using the same criteria described previously to assign animals to the groups (i.e., at least 1 overflight ≥85 dBA on a particular day for inclusion in the treatment group). Daily distance traveled by group (control, treatment) was not normally distributed, and therefore was ranked prior to statistical analyses (Conover 1980).

Regression Models

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

RESULTS

Noise Exposure

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

The SELs were measured or estimated for each overflight. For animals under direct observation, SELs ranged from 46 to 127 dBA; the maximum noise exposure was produced by an F-15 flying at a slant distance of 106 m from the caribou. The mean SEL for all 159 overflights was 98 dBA (Table 1). F-15s produced the greatest SELs ($\bar{x}$ = 103 dBA), followed by F-16s ($\bar{x}$ = 96 dBA) and A-10s ($\bar{x}$ = 95 dBA). Most (>70%) overflights we observed resulted in SELs between 85 and 100 dBA. Forty-four percent of the overflights were in the 90–100 dBA range; <10% of the overflights exceeded 110 dBA.

Activity Cycles

Three of 9 VHF transmitters malfunctioned during late winter, which left 5 animals in the treatment group but only 1 in the control group. Nine collars were deployed during the insect season: 4 on animals in the treatment group and 5 on animals in the control group. One collar

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

Table 1. Flight characteristics and estimated sound exposure levels (SEL) of low-altitude overflights of caribou by military jet aircraft in Alaska, 1991. dBA = A-weighted scale in decibels representing the sensitivity of normal human hearing; n = number of caribou groups (≥1 caribou) subjected to overflights.

		Slant distance (m)		Airspeed (km/hr)		SEL (dBA)		
Aircraft	Season	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	n
A-10	Late winter	375	28.4	470	3.8	99	1.1	77
	Postcalving	448	55.0	530	7.8	94	1.0	66
	Insect	749	221.9	526	12.0	90	2.5	24
	All	457	101.8	501	7.9	95	1.5	167
F-15	Late winter	538	76.4	659	23.6	106	2.3	28
	Postcalving	1,606	330.5	560	50.4	96	1.1	27
	Insect	1,414	308.3	693	8.9	105	2.0	34
	All	1,197	238.4	642	27.6	103	1.8	89
F-16	Insect	1,647	244.7	807	22.0	96	3.0	12
All		756	180.7	562	18.3	98	1.8	268

on an animal in the control group failed 3 days after the start of the sampling period, and another control animal wandered out of range and was not relocated until 3 days before the end of the sampling period; these animals were not used in analyses. Ten collars were deployed during postcalving; 3 of 5 caribou in the control group wandered into the treatment area and were exposed to overflights by low-altitude jet aircraft. Thus, 8 animals were overflown, and only 2 animals were not exposed to overflights during this sampling period.

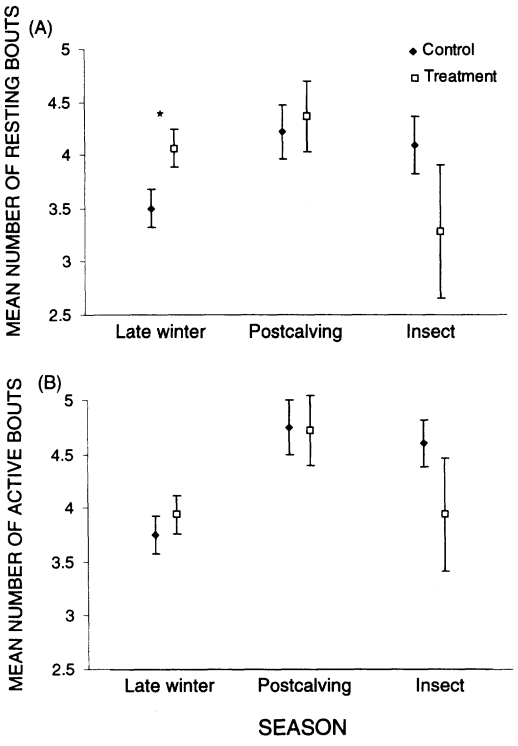

Fig. 2. Comparisons (ANOVA) of daily number ($\bar{x} \pm$ SE) of (A) resting and (B) active bouts for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. An asterisk denotes a difference between control and treatment groups ($P \leq 0.05$).

The number of resting bouts per day for animals in the control group ranged from 3.5 to 4.2 during the 3 sampling periods (Fig. 2A). Caribou in the treatment group had more ($F_{1,31}$ = 3.99, P = 0.05) resting bouts per day during late winter than caribou in the control group. The number of active bouts per day for animals in the control group ranged from 3.8 to 4.8 (Fig. 2B).

The mean length of resting bouts for animals in the control group ranged from 1.4 to 3.8 hr during the 3 sampling periods (Fig. 3A). The mean length of resting bouts during the insect season for animals from the treatment group was shorter than the control group ($F_{1,46}$ = 6.11, P = 0.02). The mean length of active bouts for animals in the control group ranged from 2.3 to 4.6 hr (Fig. 3B). Mean length of active bouts recorded for animals in the treatment group did not differ ($F_{1,46}$ = 3.28, P = 0.08) during any of the sampling periods, although there was a consistent trend for animals in the treatment group to have longer active bouts than animals in the control group. Both treatment and control animals had longer active bouts during the insect season than during the other 2 sampling periods ($F_{2,89}$ = 7.78, P = 0.001), with an extreme value of 6.2 hr of activity for treatment animals.

Daily time spent resting for animals in the control group ranged from 5.8 to 12.5 hr during the 3 sampling periods (Fig. 4A). Animals from

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

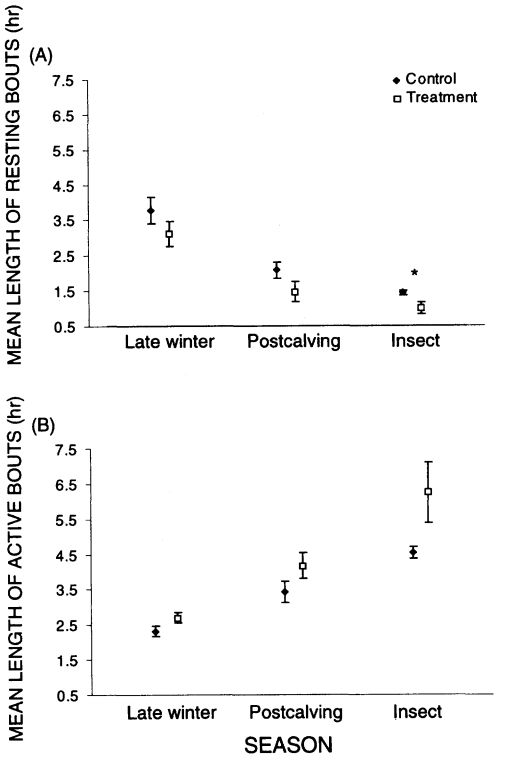

Fig. 3. Comparisons (ANOVA) of the mean length ($\bar{x} \pm$ SE) of (A) resting and (B) active bouts for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. An asterisk denotes a difference between control and treatment groups ($P \leq 0.05$).

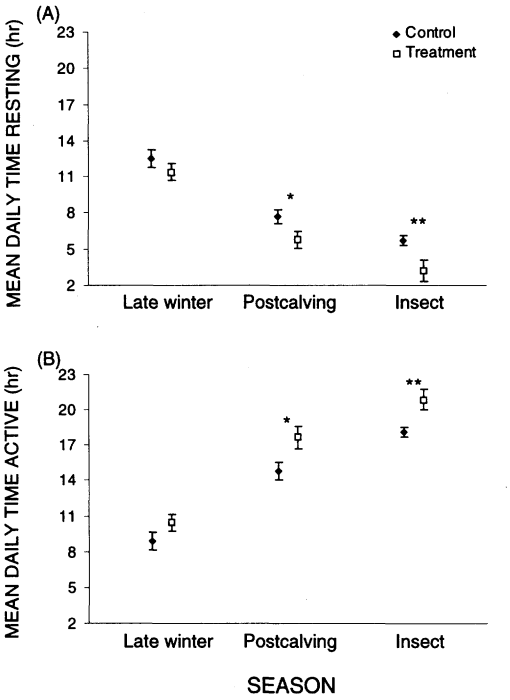

Fig. 4. Comparisons (ANOVA) of the total time ($\bar{x} \pm$ SE) spent (A) resting and (B) active for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. Number of asterisks denotes the level of significance for a particular season (i.e., * = $P \leq 0.05$; ** $P \leq 0.01$).

the treatment group spent less time resting during both postcalving ($F_{1,52} = 3.82$, $P = 0.05$) and the insect season ($F_{1,46} = 6.41$, $P = 0.01$), whereas there was no difference during late winter ($F_{1,31} = 1.10$, $P = 0.30$). Trends in daily time spent active were the reciprocal of time spent resting. For the control group, daily time active ranged from 11.5 (estimated value) to 18.1 hr (Fig. 4B). For the treatment group, daily time spent active was greater during both postcalving ($F_{1,52} = 3.64$, $P = 0.03$) and the insect season ($F_{1,46} = 7.51$, $P = 0.01$). A similar trend of greater daily time spent active for treatment animals was apparent during late winter, but the difference in this season was not significant ($F_{1,31} = 1.99$, $P = 0.17$). In the extreme, treatment animals were active for an average of 21 hr/day during the insect season.

Daily activity counts for control animals ranged from 3,288 during late winter to 28,179 during the insect season, illustrating substantial seasonal differences in activity. Proportional activity counts (i.e., total counts per day/total counts per season) for control animals, however, were 0.17 in all seasons (Fig. 5). Animals from the treatment group had higher overall daily activity levels (i.e., higher proportional activity counts) only during postcalving ($F_{1,52} = 7.63$, $P = 0.01$). The proportional total count for treat-

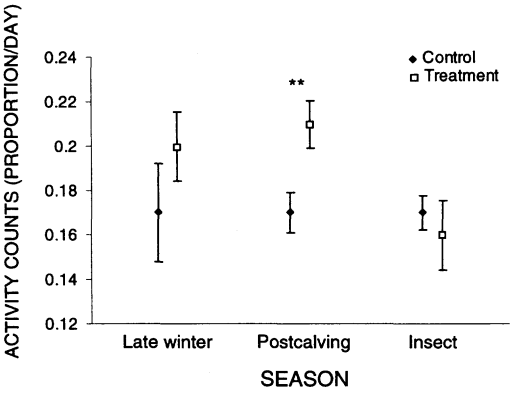

Fig. 5. Comparisons (ANOVA) of proportional total counts (i.e., counts per day/total counts per season; $\bar{x} \pm$ SE) for control and treatment (i.e., exposed to overflights by low-altitude jet aircraft) caribou in Alaska, 1991. Double asterisks denote a difference between control and treatment groups ($P \leq 0.01$).

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

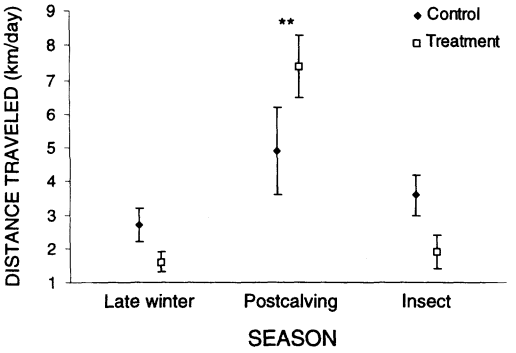

Fig. 6. Comparisons (ANOVA) of daily distance ($\bar{x} \pm$ SE) traveled (km) for control and treatment (i.e., exposed to overflights by low-altitude aircraft) caribou in Alaska, 1991. Double asterisks denote a difference between control and treatment groups ($P \leq 0.01$).

ment animals during postcalving was 0.21, which translates to an actual count of 35,051. A similar trend of higher counts for treatment animals also was apparent in late winter ($F_{1,22}$ = 0.87, P = 0.36).

Movements

Distances traveled by treatment animals did not differ from distances traveled by control animals during late winter ($F_{1,36}$ = 0.51, P = 0.48) and during the insect season ($F_{1,39}$ = 0.45, P = 0.51; Fig. 6). During postcalving, however, treatment animals traveled farther than did control animals ($F_{1,38}$ = 5.37, P = 0.01).

Regression Models

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

During late winter, all 3 response variables associated with resting were significantly related to noise exposure. Specifically, the number of resting bouts was related to the number of overflights [NF; number of resting bouts = 3.53 + 0.061 (NF), r^2 = 0.52; $F_{1,23}$ = 5.81, P = 0.03], mean duration of resting bouts was related negatively to number of overflights [4.37 − 0.130 (NF), r^2 = 0.50; $F_{1,23}$ = 5.63, P = 0.03], and the daily time spent resting was related negatively to the time-averaged noise level [L_T; 14.0 − 0.032 (L_T), r^2 = 0.46; $F_{1,23}$ = 6.98, P = 0.04].

During postcalving, none of the regression models relating resting cycles to noise were statistically significant ($F_{1,31}$ = 3.37, P = 0.08), and the amount of variation explained by all of the models was low. Similarly, none of the models for the insect season were significant ($F_{1,10}$ = 2.99, P = 0.12), although the amount of variation explained by 2 of the models was approximately 50%.

Regression models relating daily distance moved by treatment animals to various noise variables were not significant ($F_{1,23}$ = 0.46, P = 0.51) during late winter and the insect season ($F_{1,10}$ = 0.18, P = 0.68); however, a highly significant model was produced during postcalving. This model selected the loudest overflight of the day (LSEL) as the best variable to account for variation in daily distance moved ($F_{1,31}$ = 4.72, P = 0.003; distance moved = 1.39 + 0.476 (LSEL), r^2 = 0.52).

DISCUSSION

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

We also are concerned that aircraft disturbance could have deleterious effects on daily energy balance in years when range quality is low, particularly during the insect season. Summer nutrition is critical for gains in body mass necessary for successful reproduction (Allaye-Chan 1991, Cameron et al. 1993, Cameron 1994, Cameron and Ver Hoef 1994) and survival through winter (Albon et al. 1983, Clutton-Brock et al. 1983). Female caribou subjected to

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

severe insect harassment enter rut in poorer condition and may not achieve the body mass necessary for successful conception (Cameron et al. 1993, Cameron 1994, Cameron and Ver Hoef 1994, Gerhart et al. 1997). Survival of male and female caribou through winter also can be compromised by severe insect harassment (White et al. 1975), and disturbance by jet aircraft may exacerbate the situation when caribou are energetically stressed. Long-term data on body mass of 10-month-old female caribou of the Delta Herd (Valkenburg 1994), for example, indicate that the average body mass of caribou was at the lowest point recorded (i.e., 52 kg compared with the long-term average of 60 kg) in 1991, suggesting that the animals we studied that year may have been vulnerable to the potentially exacerbating effects of human disturbance.

Activity Cycles

Of the 7 variables related to daily cycles of activity, we think duration of bouts and daily time spent active and resting were the most useful variables for assessing effects of overflights. These variables most accurately reflect the way caribou balance energy intake with output. Daily activity counts integrate total activity for the entire day and are useful for comparison among days, particularly for animals with both treatment and control days, and for comparisons between seasons.

The activity cycles of undisturbed caribou (i.e., animals which were not subjected to overflights on a given day) indicated caribou were least active during late winter (11.2 hr/day), more active during postcalving (14.8 hr/day), and most active during the insect season (18.1 hr/day; Fig. 4B). Activity counts collected with a mercury tip-switch are subject to freezing at temperatures $<-32°C$ (Maier et al. 1996), which could partially account for the lower counts in late winter. Nonetheless, the lower activity counts in winter are most likely due to decreased activity. Activity counts still were registering although temperatures were $<-30°C$ during the night. No counts would register if the tip-switch were frozen (Maier et al. 1996).

Although the intensity of responses to low-altitude overflights differed by season, treatment animals exhibited consistent trends of increased activity and decreased resting compared with control animals during all 3 sampling periods. In late winter, a significant increase in the number of daily resting bouts (Fig. 2A) was associated with a near significant ($P = 0.08$) increase in mean duration of active bouts (Fig. 3B). The trend toward increasing activity by treatment animals was stronger for postcalving caribou and resulted in a significant decrease in daily time spent resting (Fig. 4A), and a 2.8-hr increase in daily time spent active (Fig. 4B). Daily activity counts of treatment animals also increased compared with control animals in the postcalving period (Fig. 5). During the insect season, treatment animals had shorter resting bouts (1.4 hr) and longer active bouts (3.4 hr) than did control animals. Daily time spent active for treatment animals (20.1 hr) was at an extreme for all conditions evaluated (Fig. 4B). Thus, although instantaneous behavioral responses to overflights were mild (Murphy et al. 1993), long-term responses and effects of overflights were evident in daily cycles of activity.

Movements

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

In the postcalving period, treatment animals traveled significantly farther than did control animals. These results suggest the presence of newborn calves in June causes female caribou to respond more strongly to disturbance than at other times of the year. This increased movement during postcalving corresponds with the increased activity level discussed previously and suggests caribou with young calves are more likely to move in response to disturbance than at other times of the year. This increased movement in response to overflights was not detected in analyses of caribou activity budgets (Murphy et al. 1993). There are no data to evaluate whether treatment animals during postcalving were trying to move from the impact zone. Dau and Cameron (1986), however, demonstrated

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

that caribou with neonatal calves will avoid areas with disturbing stimuli.

The increased movement observed during postcalving probably was of low energetic cost because caribou moved only an additional 2.5 km/day, and because the energetic costs of locomotion for caribou are lower than for any other ungulate evaluated to date (Fancy and White 1987). If caribou moved to less productive habitat, however, there would be additional costs, as was demonstrated for bighorn sheep (Bleich et al. 1990, 1994). In addition, small changes in habitat quality can have multiplicative effects on caribou productivity (White 1983). Changes in distance moved and habitat use also may change the probability of encountering predators (Sih 1984). Harrington and Veitch (1992) reported that females exposed to overflights were more likely to lose their calves. Nevertheless, they were not able to determine whether these calves actually died or simply were separated from their radiocollared mother. If overflights increase chances that caribou will encounter predators or increase chances of newborn calves being separated from their mothers, thereby increasing their vulnerability to starvation or predation, then these potential consequences of aircraft disturbance could lead to population-level effects and should be investigated more thoroughly.

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

Regression Models

Models of daily resting cycles from activity counts and daily movements of treatment animals regressed against 3 measures of noise exposure were developed to evaluate whether any specific aspect of noise was responsible for observed variations in behavior or movements. Resting variables were significantly related to noise variables in late winter, and the number of resting bouts increased with the number of overflights. Mean duration of resting bouts declined with number of overflights, while daily time spent resting declined with time-averaged noise level. Caribou were sensitive to aircraft overflights in late winter as indicated by interrupted lying bouts; however, there was no associated increase in activity, probably because of the high cost of traveling through snow. The most robust model resulted from the postcalving season, when the loudest overflight of the day was highly correlated with variation in daily movements. Caribou with neonatal calves responded to loud overflights by increasing movement and leaving the impact area. Significant models were deduced in late winter and postcalving seasons; however, $\leq$52% of the variability in patterns of activity and movements was accounted for by these models. Abiotic variables such as snow depth, temperature, precipitation, and wind speed, and biotic variables including body condition, pregnancy status, habitat quality and availability, group size, and insect harassment influence movements and activity of caribou (White et al. 1975, Skogland 1984, Russell et al. 1993), and may account for the remaining 42% of the variation. We believe the effect of harassment by insects transcends those due to overflights to the extent we could not deduce specific relations between activity or movements of caribou and noise variables during the insect season.

Results of this study may have been considerably different if we had chosen to work with a herd that had little or no previous exposure to overflights by low-altitude aircraft. A herd

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

without opportunity to habituate probably would have had stronger reactions than those demonstrated by the Delta Herd. The responses of a naive population would be of great interest; however, in studying a population that has had an opportunity to habituate to aircraft disturbance, we addressed what long-term effects are likely to be. In their study of mountain sheep, Bleich et al. (1994) found sheep did not habituate to helicopter overflights. However, ungulates typically respond more strongly to overflights by helicopters than to overflights by light or jet aircraft, and either may require a longer period of habituation or may not habituate to any extent to this disturbance (Bleich et al. 1994).

MANAGEMENT IMPLICATIONS

Overall, the results of this study indicate that reactions to overflights were mild, but that modifications of activity cycles and daily movements were evident. For the 3 seasons evaluated, severity of responses to overflights was inversely related to age of calves accompanying females under study (i.e., responses were strongest when young calves were present). Therefore, we infer that females with young were more sensitive to aircraft disturbance. Accordingly, mitigation of military training exercises should be a priority during calving and postcalving, which occur during May and June in interior Alaska.

The finding that the Delta Herd had reached a low point in its population growth and individual animal condition (Valkenburg 1994) also may have contributed to the benign responses exhibited. Delta caribou were likely engaging in a time-minimizing versus energy-maximizing grazing strategy, particularly in late winter. Consequently, the results of this study may reflect the response of a nutritionally stressed herd rather than the response of habituated individuals. Attempts to mitigate the effects of military training exercises must necessarily embody awareness of nutritional and seasonal aspects of the life cycle of caribou.

ACKNOWLEDGMENTS

This project was funded by the USAF Noise and Sonic Boom Impact Technology Program (NSBIT). We thank Lt-Colonel R. C. Kull, Jr. (USAF) and his predecessors, Major M. M. Thompson (USAF-retired) and J. Scott, for their input and support of this research program. We thank K. Higgs and P. Freidman of the Institute of Arctic Biology (IAB), University of Alaska Fairbanks; C. Cranor of ABR and D. Barber and P. Chavez of BBN Systems and Technologies for their help with data collection; G. Zusi-Cobb of ABR for logistical support; Major N. Sharra (USAF), Sergeant J. Regan (USAF), and Sergeant Gower (U.S. Army), who served as our forward ground air controllers. We are particularly indebted to the USAF pilots who gamely followed our instructions to fly their planes in extremely precipitous terrain, and to the pilots from Tamarack Air, Caribou Air, Cassaron Helicopters, Tundra Copters, Heli-lift, and Soloy Helicopters for providing expert flying services under difficult conditions. We are grateful to N. Mosso and D. R. Klein of the Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, who were instrumental in keeping this program on track. H. A. Maier and V. A. Baxter helped retrieve Wildlink collars at the end of each sampling period. We also are indebted to the ADFG for permitting us to use their radio frequencies for radiotracking and for providing expert personnel for capturing and collaring animals. P. Valkenburg and K. Whitten aided in all of the capturing of caribou, and we thank them for their time and expertise. This manuscript was improved by the reviews of R. T. Bowyer, R. D. Cameron, K. L. Gerhart, D. R. Klein, H. A. Maier, and 2 anonymous reviewers. P. X. Quang provided expert statistical advice.

LITERATURE CITED

ALBON, S. D., B. MITCHELL, AND B. W. STAINES. 1983. Fertility and body weight in female red deer: a density dependent relationship. Journal of Animal Ecology 52:969–980.

ALLAYE-CHAN, A. C. 1991. Physiological and ecological determinants of nutrient partitioning in caribou and reindeer. Dissertation, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

AMERICAN NATIONAL STANDARDS INSTITUTE (ANSI). 1990. Sound level descriptors for determination for compatible land use. ANSI S12.40-1990/ASA 88-1990. Acoustical Society of America, New York, New York, USA.

BLEICH, V. C., R. T. BOWYER, A. M. PAULI, M. C. NICHOLSON, AND R. W. ANTHES. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. Biological Conservation 70:1–7.

———, ———, ———, R. L. VERNOY, AND R. W. ANTHES. 1990. Responses of mountain sheep to helicopter surveys. California Fish and Game 76: 197–204.

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

BOERTJE, R. D. 1985. Seasonal activity of the Denali caribou herd, Alaska. Rangifer 5:32–42.

CALEF, G. W., E. A. DEBOCK, AND G. M. LORTIE. 1976. The reaction of barren-ground caribou to aircraft. Arctic 29:201–212.

CAMERON, R. D. 1994. Reproductive pauses by female caribou. Journal of Mammalogy 75:10–13.

———, W. T. SMITH, S. G. FANCY, K. L. GERHART, AND R. G. WHITE. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

———, AND J. M. VER HOEF. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58:674–679.

CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology 52:367–383.

CONOVER, W. J. 1980. Practical nonparametric statistics. Second edition. John Wiley & Sons, New York, New York, USA.

CÔTÉ, S. D. 1996. Mountain goat responses to helicopter disturbance. Wildlife Society Bulletin 24: 681–685.

DAU, J. R., AND R. D. CAMERON. 1986. Effects of a road system on caribou distribution during calving. Rangifer, Special Issue 1:95–101.

DAVIS, J. L., P. VALKENBURG, AND R. D. BOERTJE. 1985. Disturbance and the Delta Caribou Herd. Proceedings of the North American Caribou Workshop 1:2–6.

FANCY, S. G., AND R. G. WHITE. 1985. The incremental cost of activity. Pages 143–159 *in* R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA.

———, AND ———. 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology 65:122–128.

FLEISCHMAN, S. J. 1990. Lichen availability on the range of an expanding caribou (*Rangifer tarandus*) population in Alaska. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

GERHART, K. L., D. E. RUSSELL, D. VAN DE-WETERING, R. G. WHITE, AND R. D. CAMERON. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. Journal of Zoology, London 242:17–30.

GLADWIN, D. N., D. A. ASHERIN, AND K. M. MANCI. 1987. Effects of aircraft noise and sonic booms on fish and wildlife: results of a survey of U.S. Fish and Wildlife Service endangered species and ecological services field offices, refuges, hatcheries, and research centers. U.S. Fish and Wildlife Service, National Ecology Research Center, Publication NERC-88/30.

GUNN, A., F. L. MILLER, R. GLAHOLT, AND K. JINGFORS. 1985. Behavioral responses of barren-ground caribou cows and calves to helicopters on the Beverly Herd calving grounds, Northwest Territories. Proceedings of the North American Caribou Workshop 1:10–14.

HARRINGTON, F. H., AND A. M. VEITCH. 1991. Short-term impacts of low-level jet fighter training on caribou in Labrador. Arctic 44:318–327.

———, AND ———. 1992. Calving success of woodland caribou exposed to low-level jet overflights. Arctic 45:213–218.

KRAUSMAN, P. R., AND J. J. HERVERT. 1983. Mountain sheep responses to aerial surveys. Wildlife Society Bulletin 11:372–375.

———, B. D. LEOPOLD, AND D. L. SCARBROUGH. 1986. Desert mule deer response to aircraft. Wildlife Society Bulletin 14:68–70.

———, M. C. WALLACE, D. W. DEYOUNG, M. E. WEISENBERGER, AND C. L. HAYES. 1993. The effects of low-altitude jet aircraft on desert ungulates. Pages 471–478 *in* M. Vallet, editor. Proceedings of the sixth international congress—noise as a public heath problem, Volume 3, Noise and Man '93. Nice, France.

KUNKEL, K. E., R. C. CHAPMAN, L. D. MECH, AND E. M. GESE. 1991. Testing the Wildlink activity-detection system on wolves and white-tailed deer. Canadian Journal of Zoology 69:466–469.

LAUNDRÉ, J. W., T. D. REYNOLDS, S. T. KNICK, AND I. J. BALL. 1987. Accuracy of daily point relocations in assessing real movement of radio-marked animals. Journal of Wildlife Management 51:937–940.

MACARTHUR, R. A., V. GEIST, AND R. H. JOHNSON. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. Journal of Wildlife Management 46:351–358.

———, R. H. JOHNSON, AND V. GEIST. 1979. Factors influencing heart rate in free-ranging bighorn sheep: a physiological approach to the study of wildlife harassment. Canadian Journal of Zoology 57:2010–2021.

MAIER, J. A. K. 1996. Ecological and physiological aspects of caribou activity and responses to aircraft overflights. Dissertation, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

———, H. A. MAIER, AND R. G. WHITE. 1996. Effects of ambient temperature on activity monitors of radiocollars. Journal of Wildlife Management 60:393–398.

MECH, L. D., K. E. KUNKEL, R. C. CHAPMAN, AND T. J. KREEGER. 1990. Field testing of commercially manufactured capture collars on white-tailed deer. Journal of Wildlife Management 54: 297–299.

MURPHY, S. M., AND J. A. CURATOLO. 1987. The effects of pipelines, roads, and traffic on the movements of caribou, *Rangifer tarandus*. Canadian Field-Naturalist 100:218–224.

———, R. G. WHITE, B. A. KUGLER, J. A. KITCHENS, M. D. SMITH, AND D. S. BARBER. 1993. Behavioral effects of jet aircraft on caribou in Alaska. Pages 479–486 *in* M. Vallet, editor. Proceedings of the sixth international congress—noise as a public heath problem, Volume 3, Noise and Man '93. Nice, France.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1985. Applied linear statistical models: regression, analysis of variance, and experimental design. Richard D. Irwin, Homewood, Illinois, USA.

ROBY, D. D. 1978. Behavioral patterns of barren-ground caribou of the Central Arctic Herd adjacent to the Trans-Alaska oil pipeline. Thesis, Uni-

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions

versity of Alaska Fairbanks, Fairbanks, Alaska, USA.

RUSSELL, D. E., A. M. MARTELL, AND W. A. C. NIXON. 1993. Range ecology of the Porcupine Caribou Herd in Canada. Rangifer, Special Issue 8: 1–167.

SAS INSTITUTE. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

SIH, A. 1984. The behavioral response race between predator and prey. American Naturalist 123:143–150.

SKOGLAND, T. 1984. Wild reindeer foraging-niche organization. Holarctic Ecology 7:345–379.

STOCKWELL, C. A., G. C. BATEMAN, AND J. BERGER. 1991. Conflicts in national parks: a case study of helicopters and bighorn sheep time budgets at the Grand Canyon. Biological Conservation 56: 317–328.

VALKENBURG, P. 1994. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Project W-24-2, Progress Report.

———, AND J. L. DAVIS. 1985. The reaction of caribou to aircraft: a comparison of two herds. Proceedings of the North American Caribou Workshop 1:7–9.

WEISENBERGER, M. E., P. R. KRAUSMAN, M. C. WALLACE, D. W. DEYOUNG, AND O. E. MAUGHAN. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. Journal of Wildlife Management 60:52–61.

WHITE, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

———, B. R. THOMSON, T. SKOGLAND, S. J. PERSON, D. E. RUSSELL, D. F. HOLLEMAN, AND J. R. LUICK. 1975. Ecology of caribou at Prudhoe Bay, Alaska. Pages 151–201 *in* J. Brown, editor. Ecological investigations of the tundra biome in the Prudhoe Bay region. Biological Papers of the University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Received 6 June 1996.
Accepted 13 October 1997.
Associate Editor: Hobbs.

ECOLOGICAL COSTS OF FERAL PREDATOR CONTROL: FOXES AND RABBITS

PETER B. BANKS,[1] Institute of Wildlife Research, School of Biological Sciences, A08, University of Sydney, NSW 2006, Australia
CHRISTOPHER R. DICKMAN, Institute of Wildlife Research, School of Biological Sciences, A08, University of Sydney, NSW 2006, Australia
ALAN E. NEWSOME, Commonwealth Scientific and Industrial Research Organization Division of Wildlife and Ecology, P.O. Box 84 Lyneham, ACT 2602, Australia

Abstract: We used a predator removal experiment to examine the role of red fox (*Vulpes vulpes*) predation in suppressing rabbit (*Oryctolagus cuniculus*) population growth in Namadgi National Park in southeastern Australia. At 2 sites, fox abundance was reduced with a 1080 poisoning campaign maintained over 18 months. The responses of rabbit populations in these fox-reduced sites were compared to 2 other sites where fox populations remained intact. In the 2 removal sites, rabbit populations grew to 6.5 and 12.0 times their initial population size within 18 months. In the untreated sites, rabbit populations showed very small population increases over the same period. The experiment demonstrated that 1 introduced pest species suppressed the population growth of another pest species. As fox removal was initially planned to protect native fauna threatened by fox predation, the response of the rabbits represents a serious ecological cost of fox control.

JOURNAL OF WILDLIFE MANAGEMENT 62(2):766–772

Key words: Australia, European rabbit, *Oryctolagus cuniculus,* predator effect, predator–prey, red fox, removal experiment, vertebrate pests, *Vulpes vulpes.*

The red fox (hereafter, fox) was introduced into Australia in the 1850s and quickly became a major pest species across the southern half of the continent (Rolls 1969). This species is implicated in the decline or extinction of 23 species of native small- and medium-sized mammals and currently is listed as a significant threat to 30 species of endangered or vulnerable mammals and birds (Saunders et al. 1995). The fox also is a significant predator of domestic stock, in particular sheep and lambs, and can

[1] E-mail: peter@bio.usyd.edu.au

This content downloaded from 128.227.226.203 on Thu, 5 Jun 2014 12:10:44 PM
All use subject to JSTOR Terms and Conditions