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Warren G. Eastland; R. Terry Bowyer; Steven G. Fancy

Journal of Mammalogy, Vol. 70, No. 4. (Nov., 1989), pp. 824-828.

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- TABER, R. D., AND I. MCT. COWAN. 1971. Capturing and marking wild animals. Pp. 277–317, in *Wildlife management techniques*. Third ed. (R. H. Giles, ed.). Wildl. Soc., Washington, D.C., 633 pp.
- TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *J. Wildl. Mgmt.*, 38:459–472.
- WAINWRIGHT, L. C. 1969. A literature review of cottontail rabbit reproduction. *Colorado Div. Game, Fish, Park, Spec. Rep.*, 19:1–24.

Submitted 24 February 1988. Accepted 25 January 1989.

J. Mamm., 70(4):824–828, 1989

EFFECTS OF SNOW COVER ON SELECTION OF CALVING SITES BY CARIBOU

WARREN G. EASTLAND, R. TERRY BOWYER, AND STEVEN G. FANCY

Institute of Arctic Biology, and Department of Biology and Wildlife, Room 211, Irving Building, University of Alaska, Fairbanks, AK 99775 (WGE, RTB)
U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center, 101-12th Avenue, Box 20, Fairbanks, AK 99701 (SGF)

Results of previous studies of effects of snow cover on selection of calving sites by barren-ground caribou (*Rangifer tarandus*) within traditional areas have conflicted. Lent (1980) used satellite imagery to suggest a positive correlation between specific calving zones and snow-free areas for caribou. His conclusions, however, were based on 1972–1973 data for calving and snow-cover imagery from 1978. Conversely, E. S. Fleck and A. Gunn (in litt.) reported that caribou in the Bathurst, Beverly, and Kaminuriak herds in Canada calved in areas where snow persisted the longest. We reexamined the relationship between snow cover on the calving ground of the Porcupine Caribou Herd and locations of calving concentrations for a 14-year period, and tested for differences in selection of snow-cover categories by females.

The calving ground of the 170,000-member Porcupine Caribou Herd extends from the Babbage River in Canada to the Canning River in Alaska (Fancy et al., 1989). Elevations range from sea level to about 600 m in the foothills of the Brooks Range (Fig. 1). The predominant vegetation on the calving ground is tundra and low-growing shrubs with some taller *Salix* sp. growing along the braided, low-gradient rivers. Other genera of plants on the area include *Arctagrostis*, *Betula*, *Carex*, *Dryas*, *Eriophorum*, *Equisetum*, *Lupinus*, and *Saxifraga*; plant nomenclature follows Hultén (1968).

Snow cover on the calving ground from 1974 to 1987 was determined primarily from Tiros-N satellite images (1:5,000,000 scale) archived at the Geophysical Institute, University of Alaska, Fairbanks. Snow cover was categorized as >75%, 25–75%, and <25%. Other satellite imagery with higher resolution was available for a limited number of days and was used to supplement Tiros-N imagery.

On a 1:1,000,000 map of the calving ground, we defined 20 ground units (\bar{X} = 790 km², *SD* = 421 km², range = 258–2,002 km²) from distinct geographical features visible on the Tiros-N satellite photographs and categorized snow cover for each ground unit (Fig. 1). Major rivers were used as east–west boundaries of the units; north–south boundaries were defined by elevational gradients. All areas were measured from these maps with a computerized planimeter.

Information on snow cover was compared with that of maps of concentrated calving areas (\bar{X} = 2,090 km², *SD* = 836 km², range = 381–3,345 km²) derived from data gathered about 5 June each year (G. W. Garner and P. E. Reynolds, in litt.); these data document extreme variation in locations of concentrated calving among years. Pregnant females usually arrive at their intended sites of calving during the last days of May or early June and remain near their calving sites for 7–10 days (K. R. Whitten, pers. comm.). We, therefore, compared locations of concentrated calving areas to snow-cover maps for 1 June, when most cows were arriving on the calving grounds. Clouds sometimes obscured classes of snow cover for ground units on

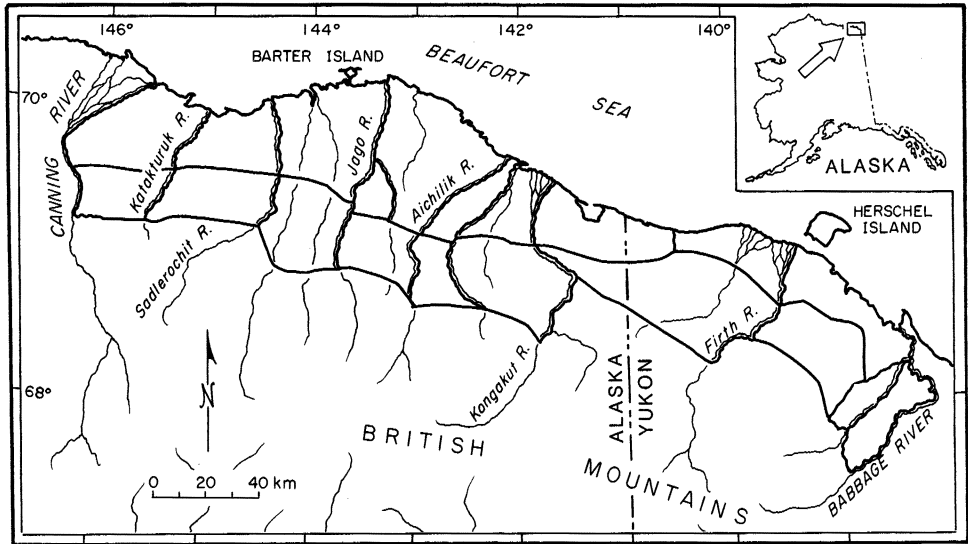


FIG. 1.—Location of ground units used for classifying snow cover on the calving ground of the Porcupine Caribou Herd in northeast Alaska and western Canada, 1974–1987.

1 June, so occasional interpolation of snow cover from adjacent days was required. High-resolution imagery (1:1,000,000) was used whenever available to ensure reliability of estimates of snow cover.

Maps of concentrated calving areas were overlaid on the ground-unit map (Fig. 1) and the proportional amount of snow cover was determined for each unit. An index was calculated comparing snow-cover use to availability $[(\text{use}/\text{availability}) - 1]$. Use was the proportion of each snow category within the concentrated calving areas for each year. Availability was the proportion of each snow-cover category on the coastal plain. Parturient females enter the coastal plain from the east. Availability was based on the area of coastal plain as far west as calving was confirmed in each year to avoid counting the westernmost end of this area as being available for calving when caribou did not travel that far. Negative values of the index indicated coverage of a snow category within the concentrated calving areas was less than proportional coverage of the available calving ground; positive values indicated coverage to a greater degree; and values of zero indicated equivalent proportions. The *G*-test of independence (Zar, 1984) was used to determine if differences between snow-cover use and availability among years were significant.

Proportion of snow cover in the concentrated calving area (\hat{Y}) was regressed against weather variables (X_i). Weather data from Barter Island (Nat. Oceanic and Atmos. Adm., Nat. Climatic Data Center, Asheville, NC) were selected for alternate days from 22 May through 5 June. Absolute values for climatic variables may differ between Barter Island and the calving ground. We believe, however, that data from Barter Island provided reliable indices to weather on the arctic coastal plain, where there were no permanent weather stations. Daily minimum temperature, daily maximum temperature, average daily temperature, daily snow on ground, daily snow fall, average daily wind vector, average daily wind speed, fastest daily wind speed, average daily cloud cover, and derived variables (e.g., average daily temperature change, difference between wind vector and wind speed) were among 102 climatic variables examined.

Variables considered for the model were examined for independence, linearity, and normality; those departing from assumptions required for regression analysis were deleted or transformed (Neter et al., 1985). Formal testing for multicollinearity, including examination of variance-inflation factors and partial coefficients of regression, was completed after the model was built (Bowyer et al., 1988; Neter et al., 1985).

Data for 10 years between 1974 and 1987 were used in these analyses (Table 1); 1982, 1984, and 1985 were excluded because not all categories of snow cover were present on the coastal plain, and 1980 was excluded because no concentrated calving area was mapped. Proportionally more area of >75% snow cover was used for concentrated calving, whereas proportionally less area of <25% snow cover was used for such activity (Table 1). A potential lack of precision in delimiting these areas, however, precludes direct statistical comparisons. Consequently, we compared number of positive, zero, and negative indices of >75% snow cover with <25% snow cover within the concentrated calving area; significant differences occurred between

TABLE 1.—*Snow cover on the Porcupine Caribou Herd calving area in northeast Alaska and northwest Canada, 1974–1979, 1981, 1983, 1986–1987.*

Snow category	Concentrated calving area			Available calving ground		
	\bar{X}	SD	Range	\bar{X}	SD	Range
>75% snow cover						
Area (km ²)	865.5	702.6	0–1,900	5,151.0	3,306.7	1,095–10,752
% of area	41.9	34.6	0–89	35.7	21.3	8–68
25–75% snow cover						
Area (km ²)	593.3	794.1	0–2,632	3,204.1	1,756.5	796–5,561
% of area	22.7	24.7	0–79	23.7	14.1	5–43
<25% snow cover						
Area (km ²)	630.9	461.9	147–1,700	5,886.6	3,931.1	2,002–11,909
% of area	35.4	28.3	7–100	40.8	26.2	16–78

levels of use and availability ($G = 7.703$, $d.f. = 2$, $P = 0.02$). The preponderance of positive values for >75% snow cover and majority of negative ones for <25% snow cover (Table 2) indicated that inclusion of >75% snow cover within the concentrated calving area was greater than its presence within the available calving ground (female caribou selected areas with greater snow cover and avoided snow-free zones for concentrated calving).

Proportion of concentrated calving areas covered by >75% snow each year was selected as the dependent variable for developing a multiple-regression model. Both true stepping and all-possible-regressions produced the same model with an $R_a^2 = 0.82$ ($SE = 14.79$, $F = 21.11$, $P = 0.001$):

$$\hat{Y} = 92.44 - 18.33X_1 + 0.26X_2$$

where \hat{Y} is proportion of the concentrated calving area of >75% snow cover, X_1 the change in temperature (°C) on 3 June ($\bar{X} = 4.3$, $SD = 1.5$, range = 2.2–7.2), and X_2 the depth (in mm) of snow on 30 May ($\bar{X} = 109.2$, $SD = 85.5$, range = 0.3–254.0). We observed no evidence of skewness, kurtosis, or lack of independence (multicollinearity) for variables included in the multiple regression, suggesting this model was apt.

Areas of >75% snow cover usually appeared as a solid snowfield on satellite imagery. From the first appearance of sufficient melt to be classed as <75%, the transition to <25% usually required 7–10 days. Ground-based 35-mm photographs taken opportunistically from 30 May to 5 June in different years were compared with snow categories assigned from satellite imagery. These photographs showed that areas of >75% snow cover were not uniform, unbroken fields of snow. Bare spots smaller than the 1-km² resolution of the satellite imagery were widely scattered throughout snowfields; thus, satellite imagery tended to overestimate snow cover. Model variables—amount of daily temperature change and depth of snow at Barter Island—probably index the number, size, and duration of bare spots in the snowfields. Local microtopography also would be expected to affect the distribution of snow-free patches.

TABLE 2.—*Indices of use of snow-cover categories for concentrated calving by the Porcupine Caribou Herd in northeast Alaska and northwest Canada. Index = (use/availability) – 1, where use is the proportion of the concentrated calving area in each snow category, and availability is the proportion of each snow category within the available coastal plain.*

Year	Snow cover		
	>75%	25–75%	<25%
1974	–1.00	–1.00	0.33
1975	0.31	–0.67	–0.65
1976	0.56	–0.73	–0.64
1977	0.17	–0.50	0.30
1978	0.63	–0.97	0.00
1979	1.27	0.82	–0.29
1981	1.50	1.44	–0.46
1983	–1.00	0.84	–0.54
1986	–0.61	–0.29	2.38
1987	0.07	0.06	–0.23

The strong positive association between zones with greater snow cover and areas of concentrated calving by caribou on the arctic coastal plain contradicts previous notions (Lent, 1980) that large, snow-free zones are used heavily for concentrated calving, and supports other findings (E. S. Fleck and A. Gunn, in litt.). Caribou selecting areas with mottled snow and an extended time of snowmelt may be influenced by both nutrition and predation, although the relative influence of one over the other may vary with time and the population dynamics of caribou.

Caribou apparently select bare ground rather than snow to give birth (Kelsall, 1968; Lent, 1980; Skoog, 1968). Parturient females use these snow-free patches within snowfields on the concentrated calving area, often one cow per bare patch when openings are small (F. J. Mauer, pers. comm.).

Postparturient caribou must meet nutritional requirements for lactation (Rognmo et al., 1983; White and Luick, 1984) to insure growth of new-born calves, and are more likely to conceive at mating when their body mass is high, indicating good physical condition (Reimers, 1983; Thomas, 1982; White, 1983). Thus, selection of areas with highly nutritious forage in a sufficient density to minimize search time is advantageous for lactating females (Kelsall, 1968; Klein, 1970, 1982; Kuropat, 1984; Kuropat and Bryant, 1980).

We hypothesize that calving caribou derive several benefits from an extended time of snowmelt. Pregnant females arrive on the calving grounds before the onset of the growing season for most forage species. *Eriophorum vaginatum* inflorescences are one of the few forages available and are at their maximum levels of nitrogen and phosphorus, lowest in percent acid-detergent fiber, and low in phenols (Kuropat, 1984; Kuropat and Bryant, 1980; Whitten and Cameron, 1980). Nutrient levels and digestibility are highest at the floral-bud stage and decline to low levels within 2 weeks of snowmelt.

As snow melts, it exposes more *Eriophorum* and reduces or eliminates energy expenditure of cratering for food by caribou (Fancy and White, 1985). This condition allows caribou to feed selectively on nutritious vegetation, and is analogous to Klein's (1982) observations concerning the influence of topographic variation and phenology of vegetation on forage quality. We postulate that dynamics of snowmelt yield *Eriophorum* inflorescences in early stages of growth for the entire duration of calving unlike areas totally free of snow. Indeed, it is well documented that snow cover affects diet selection by caribou (Adamczewski et al., 1988).

Use of bare spots by caribou in a generally snow-covered area on the coastal plain also agrees with the three ideas proposed by Bergerud and Page (1987) for caribou avoidance of predators. Predator densities are higher in foothills than on the coastal plain. Caribou that calve on the coastal plain are displaced from normal travel routes of predators and from alternative prey (Babcock, 1986). Females that use bare spots in snowfields for calving are relatively dispersed, increasing searching time by predators and reducing opportunities for surplus killing (Miller et al., 1985), especially when bare spots are small. Young calves unable to flee from predators are relatively inconspicuous on a mottled-snow background. Snowfields also might discourage avian predation because of damping effects on thermals used for soaring by predaceous birds, thereby shifting travel routes of avian predators away from calving caribou. These factors would be of importance only until completion of snowmelt.

Funding was provided by the Alaska Fish and Wildlife Research Center of the U.S. Fish and Wildlife Service in cooperation with the Alaska Cooperative Wildlife Research Unit. We are grateful to R. D. Cameron, M. P. Gillingham, R. B. Harris, D. R. Klein, T. R. McCabe, and R. G. White for their helpful comments and manuscript reviews. We also thank F. S. Chapin III, F. J. Mauer, W. J. Stringer, and K. R. Whitten for their discussions and information. We thank D. A. Borchert for providing Fig. 1.

LITERATURE CITED

- ADAMCZEWSKI, J. Z., C. C. GATES, B. M. SOUTAR, AND R. J. HUDSON. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. *Canadian J. Zool.*, 66: 1986-1996.
- BABCOCK, C. A. 1986. Vegetation patterns and microtine rodent habitat use of tundra habitats in northeastern Alaska. Unpubl. M.S. thesis, Univ. Alaska, Fairbanks, 72 pp.
- BERGERUD, A. T., AND R. E. PAGE. 1987. Displacement and dispersion of parturient caribou as anti-predator tactics. *Canadian J. Zool.*, 65:1597-1606.
- BOWYER, R. T., S. C. AMSTRUP, J. G. STAHMANN, P. REYNOLDS, AND F. BURRIS. 1988. Multiple regression methods for modeling caribou populations. *Proc. N. Amer. Caribou Workshop*, 3:89-118.
- FANCY, S. G., AND R. G. WHITE. 1985. Energy expenditures by caribou while cratering in snow. *J. Wildl. Mgmt.*, 49:987-993.
- FANCY, S. G., L. F. PANK, K. R. WHITTEN, AND W. L. REGELIN. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. *Canadian J. Zool.* 67:644-650.
- HULTÉN, E. 1968. *Flora of Alaska and neighboring territories*. Stanford Univ. Press, Stanford, California, 968 pp.
- KELSALL, J. P. 1968. The migratory barren-ground caribou of Canada. *Canadian Wildl. Serv. Monogr.*, 3:1-340.

- KLEIN, D. R. 1970. Tundra ranges north of the boreal forest. *J. Range Mgmt.*, 23:8-14.
- . 1982. Factors influencing forage quality for reindeer. Pp. 383-393, in *Wildlife-livestock relationships symposium, proceedings 10* (J. M. Peek and P. D. Dalke, eds.). Univ. Idaho, Forestry, Wildl., and Range Exp. Sta., Moscow, Idaho, 614 pp.
- KUROPAT, P. J. 1984. Foraging behavior on a calving ground in northwestern Alaska. Unpubl. M.S. thesis, Univ. Alaska, Fairbanks, 95 pp.
- KUROPAT, P. J., AND J. P. BRYANT. 1980. Foraging behavior of cow caribou on the Utukok calving ground in northwestern Alaska. *Proc. Internat. Reindeer/Caribou Symp.*, 2:64-70.
- LENT, P. C. 1980. Synoptic snowmelt patterns in arctic Alaska in relation to caribou habitat use. *Proc. Internat. Reindeer/Caribou Symp.*, 2:71-77.
- MILLER, F. L., A. GUNN, AND E. BROUGHTON. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. *Canadian J. Zool.*, 63:295-300.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1985. *Applied linear statistical models*. Second ed. R. W. Irwin, Inc., Homewood, Illinois, 1127 pp.
- REIMERS, E. 1983. Reproduction in wild reindeer in Norway. *Canadian J. Zool.*, 61:211-217.
- ROGNMO, A., K. A. MARKUSSEN, E. JACOBSEN, H. J. GRAV, AND A. S. BLIX. 1983. Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth, and mortality. *Rangifer*, 3: 10-18.
- SKOOC, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Unpubl. Ph.D. dissert., Univ. California, Berkeley, 699 pp.
- THOMAS, D. C. 1982. The relationship between fertility and fat reserves of Peary caribou. *Canadian J. Zool.*, 60:597-602.
- WHITE, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos*, 40:377-384.
- WHITE, R. G., AND J. R. LUICK. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. *J. Zool. Soc. London*, 51:215-232.
- WHITTEN, K. R., AND R. D. CAMERON. 1980. Nutrient dynamics of caribou forage on Alaska's arctic slope. *Proc. Internat. Reindeer/Caribou Symp.*, 2:159-166.
- ZAR, J. H. 1984. *Biostatistical analysis*. Second ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 718 pp.

Submitted 24 October 1988. Accepted 16 March 1989.

J. Mamm., 70(4):828-833, 1989

ROOSTING AND ECHOLOCATION BEHAVIOR OF THE AFRICAN BAT, *CHALINOLOBUS VARIEGATUS*

MARTIN OBRIST, HUGH D. J. N. ALDRIDGE, AND M. BROCK FENTON

Zoologisches Institut, Universität München, 8 München 2, Federal Republic of Germany
5 Buckingham Place, Clifton, Bristol, BS8 1LM, United Kingdom
Department of Biology, York University, North York, Ontario, Canada M3J 1P3

The vesperilionid bat *Chalinolobus variegatus* (Tomes, 1861) has been reported from savannah habitat over large areas of Africa (Smithers, 1983). Anecdotal accounts suggest that this species feeds largely on moths (Lepidoptera) they catch during continuous, slow flight (Kingdon, 1974) and that groups of them roost in foliage or thatch (Kingdon, 1974; Lang and Chapin, 1917; Pienaar et al., 1987). The timing of parturition in this species varies according to latitude, with northern populations showing a boreal cycle (parturition in March—Aellen, 1952; Allen and Lawrence, 1937; Anciaux de Faveaux, 1983) and southern ones an austral cycle (Anciaux de Faveaux, 1983; Kulzer, 1962; Smithers and Wilson, 1979; Vershuren, 1957).

Herein, we report our observations of roosting behavior, vocalizations, and timing of parturition in a group of *C. variegata* observed in Mana Pools National Park (15°44'S; 29°21'E) in Zimbabwe during November 1987. We observed roosting bats directly or through binoculars, and on two separate occasions captured them by use of a 23-cm-diameter plastic bucket on the end of a long pole.

We recorded vocalizations of individuals simultaneously with two QMC S200 bat detectors (QMC Instruments, 229 Mile End Road, London E1 4AA, England) on two tracks of a Racal Store 4D tape recorder operated at 76 cm/s; the frequency response of the complete recording system was flat (± 5 dB) between