Empirical and theoretical considerations toward a model for caribou socioecology

James L. Davis[1], **Patrick Valkenburg**[1], and **Rodney D. Boertje**[1]

Abstract: The Delta and Yanert caribou *(Rangifer tarandus granti)* herds apparently maintained discrete calving areas from 1979 through 1983 (as determined by radio telemetry studies), even though substantial intermixing occurred during other seasons. Also, the Delta herd apparently used a single traditional calving area from the 1950's through 1983, based on results of aerial surveys and 1979-83 telemetry studies. Calving distribution in 1984 changed dramatically; 5 of 25 radio-collared Delta herd cows ≥3 years old and 5 of 24 radio-collared Delta herd cows <3 years old were located in the calving area of the Yanert herd, 72 km west-southwest of the traditional Delta herd calving area. Use of traditional, separate calving areas resumed for the two herds in 1985. One implication of these data is that the current definition of a caribou herd may not always apply. A second implication is that current models of caribou socioecology, based largely on the concepts of traditional use of calving grounds, herd identity/fidelity, and dispersal, inadequately predict or explain all empirical observations. An evolving model of optimal and dynamic use of space can help refine current models of caribou socioecology.

Key words: calving, caribou, conceptual model, dispersal, herd identity, socioecology.

[1] Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701.

Rangifer, Special Issue No. 1, 1986: 103 - 109

Introduction

We believe the topic of caribou *(Rangifer tarandus)* socioecology necessitates combining empirical and theoretical science. The purpose of this paper is three-fold: (1) we present sociological data from the Delta (DCH) and Yanert caribou herds (YCH), (2) we cite examples to show that the DCH and YCH data are not sole exceptions to working conceptual models of caribou socioecology, and (3) we discuss theoretical considerations for a more complete model of caribou socioecology.

A conceptual model of caribou socioecology has never been concisely articulated and tested. Indeed, existing models are only in the minds of caribou workers. We believe that most of these models encompass little more than the following concepts: (1) *caribou herds* and (2) *traditional calving grounds* (Skoog, 1968; Thomas *et al.*, 1968), (3) *dispersal* (Skoog, 1968), and (4) *basic caribou social structure* described by Lent (1965) as a «temporary tenuous association(s) of individuals» and by Bergerud (1974*a*) as «open social units.» In contrast, Parker (1972) and Miller (1974) viewed the basic social structure as consisting of persistent nonrandom associations of adult caribou resulting from social attachment.

Consolidating the above concepts into models has resulted in existing models being mostly descriptive and focused primarily on the larger patterns of caribou socioecology. The focus on larger patterns is symptomatic of an emerging discipline (Austad and Howard, 1984). We believe it is now time to redirect the focus on caribou socioecology to include the full range of empirical observations and to expand conceptual models to include explanations of the mechanisms and functions involved in caribou socioecology. We discuss a framework of mechanisms and functions (Bergerud, 1974*a*), which has been available but not widely incorporated into conceptual models, to help explain exceptions to the larger patterns of caribou socioecology.

By monitoring movement of radio-collared caribou in the range of Alaska's DCH from 1979 through 1985, we empirically tested the concepts of herd identity, traditional calving grounds, and dispersal. These concepts have been intertwined for decades. Skoog (1968) and Thomas *et al.* (1968) conceptualized herds based on calving grounds. Skoog (1968) defined «a herd of caribou» as any group which establishes a calving area distinct from that of any other group and uses the area repeatedly over a period of years, with slight modification when deep snow persists. He elaborated that mixing between herds at other seasons may occur occasionally, but this mixing is not considered contradictory to his herd definition. Further, he believed that the herds invariably separate and return to ancestral calving grounds each spring, even though gains or losses in animal numbers may have occurred. Skoog's herd definition applies throughout this paper.

Gunn and Miller (1986) reviewed the concept of traditional calving grounds, so we do not attempt an explicit definition of «traditional» calving grounds here. For this paper, we define traditional or ancestral calving grounds only by what the terms imply.

We consider dispersal in the context of emigration/immigration as used by Skoog (1968). More specifically, for this discussion we define dispersal as any movement by a parturient female that results in (1) her calving outside the distributional range of the herd whose calving area she nsed in the preceding year, and/or (2) her calving on any traditional calving ground other than that of the herd used in the preceding year.

In recent years the need for enlightened and more intensive management of caribou (Bergerud, 1974*b*, 1980; Klein and White, 1978; Miller, 1982) and an increasing need to predict impacts of disturbance and development on caribou and their habitats (Martell and Russell, 1985) have generated a critical reevaluation of current concepts of caribou socioecology.

Methods

Radio-collaring caribou

Between 1979 and 1985, the DCH contained 4000 to 8000 caribou and the YCH contained 500 to 1000, and the herds occupied adjacent or overlapping ranges (Fig. 1). Pertinent information on the history and ranges of both herds is summarized or referenced in Davis and Valkenburg (1985).

From 1979 through 1984, we captured and radio-collared 63 female caribou from the DCH and YCH (60 of these 63 provided data for this paper).

Relocating radio-collared caribou

Radio-collared caribou were relocated from fixed-wing aircraft (Bellanca Scout and Piper Super Cub) equipped with two Yagi antennas. In most years one or more relocation flights were made each month. All radio collars were monitored audibly during each flight and an attempt was made to determine the general location of each signal that was heard. We attempted to visually relocate all collared caribou on each flight during the first several years when fewer than 30 caribou were collared and in subsequent years when logistics permitted. On flights when logistical complications precluded visual relocation of all collared caribou, those individuals which were not recently located were given first priority. Some collared caribou were sighted from the ground during June and July 1979 by Alaska Department of Fish and Game personnel conducting sheep (*Ovis dalli dalli*) studies and caribou composition counts. For each sighting, we attempted to record group size, location, presence or absence of a calf, and group composition. We received some reports from the public, including hunters, on the locations of collared caribou that were observed or shot.

Calving

Annually from 1979 through 1984, calving distribution was monitored in the ranges of the DCH and YCH using fixed-wing aircraft to relocate radio-collared females and to conduct ocular reconnaissance. Geographic separation of calving grounds of the two herds was assessed.

Methods used to monitor calving distribution in 1984 are of particular interest because of the unexpected results. Fixed-wing aircraft were used to relocate radio-collared caribou on 10, 14, 16, 18, and 26 May 1984; a 2-person ground crew classified caribou on the traditional «core» calving area on 20 - 23 May 1984; and a helicopter was used on 26 May 1984 for a composition count in the upper Wood River area (Fig. 1).

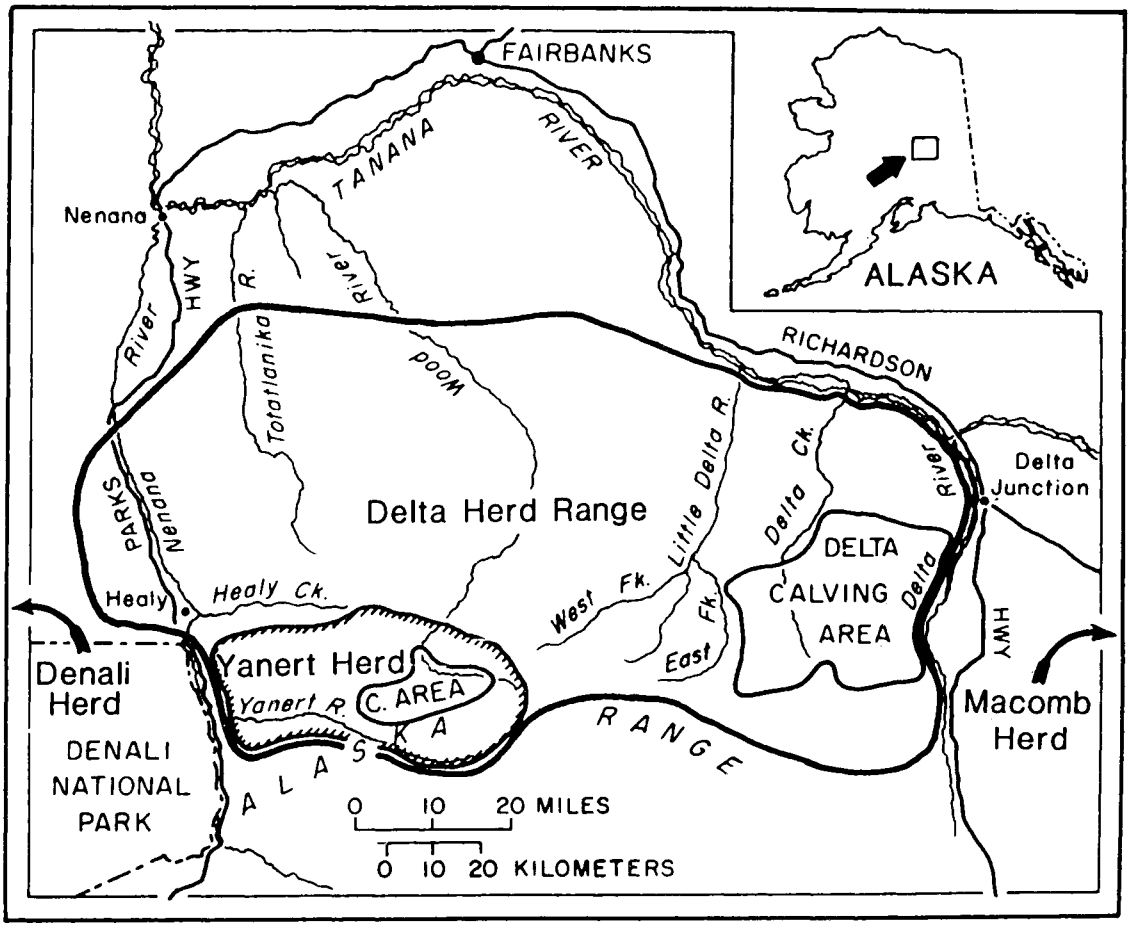

Fig. 1. Study area and distribution and calving areas of the Delta and Yanert Caribou herds.

Herd identities and fidelity

Discreteness of the DCH and the YCH, and the spatial relationships to one another and to neighboring Nelchina, Macomb, Fortymile, and Denali herds, were determined by monitoring movements and calving distribution of caribou that were radio-collared within the range of the DCH or YCH.

Results

Calving distribution

Based on results of aerial surveys and 1979-83 telemetry studies, the DCH apparently used a single calving area (i.e., one contiguous geographic area separated from the 1980-85 Yanert calving area) from the 1950's through 1983 (Fig. 1). The surveys prior to 1970 were not intensive and may not have located all calving females; however, the surveys did demonstrate annual use of the traditional DCH calving area. The DCH and YCH maintained discrete calving areas from 1979 through 1983, as determined by radiotelemetry, but significant intermixing occurred during other seasons (Davis and Valkenburg, 1985).

Numbers of radio-collared females that used the Delta and Yanert calving areas from 1979 through 1985 are listed in Table 1. Calving distribution in 1984 was of particular interest because 20% (10/49) of the radio-collared DCH females calved and/or were distributed during calving with YCH females in the Yanert calving area. Of these 10 DCH females, five were $\geq$36 months and five were <36 months old. At calving time in 1984, there was a total of 49 radio-collared females in the DCH, including 25 $\geq$36 months old and 24 <36 months old.

During calving in 1985, all radio-collared females, except one, resumed calving in their respective traditional calving grounds. The single exception (Table 1) was a caribou radio-collared

Table 1. The number of female caribou radio-collared annually from the Delta and Yanert herds and their calving range location, 1979-85.

	Delta herd[a]			Yanert herd[b]		
Year	Number radio-collared	Delta calving range	Yanert calving range	Number radio-collared	Delta calving range	Yanert calving range
1979	11	11	0	0	-	-
1980	0	11	0	0	-	-
1981	10	18	0	8[c]	0	7
1982	11	28	0	0	0	7
1983	12	39	0	0	1	6
1984	11	38	10	0	1	6
1985	0	44	0	0	1	7

[a] All radio-collared females were collared in the range of the Delta Caribou herd and assumed to be DCH members.

[b] All radio-collared females were collared in the range of the Yanert Caribou herd and assumed to be YCH members.

[c] A human recording error of radio frequencies caused one of the eight caribou collared in 1981 to not be located until 1985.

in April 1981 on the YCH's winter range. She calved in 1981 and 1982 on the Yanert calving ground, but calved on the Delta Herd's calving ground in 1983, 1984, and 1985.

Dispersal/herd identity

From 1979 through 1985, only one of 60 radio-collared females «permanently» switched between the DCH and YCH calving grounds, suggesting a 98% (59/60) fidelity of females to their calving ground. However, in 1984, 21% (10/43) of the radio-collared DCH females calved in the YCH's calving ground. The «dispersal» of DCH females in 1984 was apparently only a 1-year phenomenon because all 10 DCH cows returned to the Delta calving ground in 1985.

Even considering the relative lack of calving ground fidelity in 1984, overall fidelity to respective calving grounds has been high. Based on «calving-ground-years» for caribou ≥24 months old, the observed fidelity rate during this study has been 96% (206/214).

Discussion

Our observations of radio-collared Delta and Yanert caribou are partially consistent with conventional definitions and concepts of herds, traditional calving grounds, and dispersal. However, several of our observations indicate the need to expand and refine concepts and definitions to adequately describe and predict phenomena related to herd identity and fidelity to calving areas.

For example, we believe that the existing model(s) of caribou socioecology inadequately predicted: (1) the 1-year «abandonment», in 1984, of the traditional DCH calving ground by 20% (10/49) of the radio-collared DCH females, and (2) the permanent abandonment of the YCH calving ground by the one female. Even if we were to concede that the existing model(s) implies predictions to account for the observations, the existing model(s) certainly do not include credible triggering and functional mechanisms to explain the observations. Rather, the present model(s) labels our observations as exceptions or anomalies.

However, our observations may not be exceptions. They may be infrequent events that are typical for sizable «associations» of caribou observed for a protracted period. Radio-telemetry has provided the first opportunity to test the conventional socioecology model(s) for caribou, and results are just now becoming available. Already, the studies have revealed many «exceptions» or «anomalies». Gauthier (1984) documented temporary egress from the Burwash herd study area by 3 of 26 radio-collared caribou in 1982. In addition, monitoring

radio-collared caribou helped determine that approximately 16-19% (62-72/387) of the adults and subadults in the 1981 rutting population did not calve in the two traditional calving areas for the Burwash herd in spring 1982 (i.e., dispersal).

Similarly, monitoring radio-collared caribou helped to document the dispersal of several hundred caribou from traditional range of the Big River Herd in Alaska, and subsequent calving in nontraditional calving areas (Pegau 1985). More questions than answers have accrued regarding herd identity and traditional calving areas for caribou radio-collared on the Arctic Coastal Plain of Alaska between the calving grounds of the Western Arctic (see Davis (1980) for herd locations) and Teshekpuk herds (Davis and Valkenburg, unpublished data). Radio-telemetry has also aided in documenting frequent shifts in calving distribution in the Fortymile (Valkenburg and Davis, 1986) and Denali herds (Troyer, 1981). And telemetry has helped show that sharing a common calving ground is an inappropriate criterion for defining herds in some situations involving woodland caribou (*R. t. caribou*) (Edmonds and Bloomfield, 1984; R. Farnell, pers. comm., Yukon Wildlife Branch).

One implication of these «exceptions» or «anomalies» is that conventional concepts of traditional calving grounds, herd fidelity, and dispersal (i.e., caribou socioecology) are incomplete. We believe that current concepts must be expanded, refined, and/or revised to better explain dispersal to adjacent calving areas and exceptions to caribou calving in a «traditional» manner.

Currently, there is major debate over the complex subject of caribou socioecology. The debate focuses on three issues: (1) the basis for defining caribou herds, (2) Bergerud's (1974*a*) working hypothesis that caribou optimally and dynamically use space (including short-term shifts in calving distribution) vs. the concept of long-term selection for calving grounds (includes optimal foraging theory), and (3) the theoretical mechanisms contributing to dispersal and/or maintenance of herd discreteness (Haber and Walters, 1980).

Bergerud (1974*a*:582) introduced the concept of optimal and dynamic use of space in a discussion as follows: «However, this temporal-space optimum will soon be altered and it will be more advantageous to be elsewhere.» In discussing caribou socioecology, Bergerud (1974*a*) discussed many of the terms and concepts we believe integral to any model that satisfactorily depicts caribou socioecology.

Bergerud (1974*a*) discussed the role of facultative and obligate behavior in the phylogeny and ontogeny of caribou, and suggested that our understanding of caribou movement and aggregating behavior would be greatly enhanced if we knew how herds return to specific locations. He offered three hypotheses, which may not be mutually exclusive, to explain this phenomenon: (1) that the ability of animals to «home» to a specific area involves learning and tradition; (2) that animals are funneled by topographical features and recognize the calving grounds based on phylogenic imprinting; and (3) that animals have an orientation direction which often results in the animal reaching the same general area. Social facilitation is continually interactive with all three possibilities. Anticipatory adaptation was also discussed by Bergerud (1974*a*), but site affinity was not (albeit site affinity overlaps with learning and tradition). Herd definition was lacking in Bergerud's discussion.

Social facilitation (and/or contagious behavior) seems inescapably involved in the movement and distribution behavior of caribou. We envision a constant tug-of-war in the caribou's mind between yielding to learned/traditional movement and yielding to «group pressure» to do otherwise when the traditions differ among interacting individuals.

Studies of diverse species have shown that bimorphism or polymorphism is common in populations. The literature on invertebrates is replete with studies of morphism (e.g., Iwanaga *et al.*, 1985; Borowsky, 1985) and recent publications, regarding bi- or polymorphism, are common for birds (e.g., Ratti, 1985), fish (e.g., Jurss *et al.*, 1985), and there is increasing cognizance of bi- or polymorphism contributing to variation in large mammal populations. For example, Bunnell and Harestad (1983) concluded that observed movement patterns of black-tailed deer *(Odocoileus hemionus columbianus)* suggested the existence of two phenotypes--«nondispersers» and «dispersers.» They stated further that, «...competition for mates is an important force governing the proportions of «dispersers» to «nondispersers.»

Given that bi- or polymorphism is common

in many species and can frequently account for observed variation within populations, it does not seem improbable that morphism in caribou could account for some observed behavioral differences. Edmonds and Bloomfield (1984) recently described two different annual movement strategies for woodland caribou in Alberta. Might the two strategies stem from behavioral bimorphism? Similarly, the calving behavior that we observed in the DCH and YCH caribou, behavior which did not conform to the conventional model(s) of caribou socioecology, may be partly explainable by behavioral morphism.

To conclude, we believe that confusion has resulted from lack of standardized terminology and definitions regarding caribou socioecology. Advances in the field of socioecology have not been timely synthesized by caribou workers and have not been incorporated into the conventional model(s) of caribou socioecology. We believe the conventional model(s) of caribou socioecology is incomplete and warrants modification.

Incorporating Bergerud's (1974*a*, 1985; Bergerud *et al.*, 1984) evolving model of «optimal and dynamic use of space» into other existing models would contribute toward developing a satisfactory model. Further synthesis of the literature on the socioecology of other species will identify components required for a valid model of caribou socioecology. Implications of the following concepts will undoubtedly contribute to the evolving model: (1) intraspecific variation in social systems (Lott, 1984); (2) evolutionarily stable strategy (Maynard-Smith and Price, 1973, cited in Austad and Howard, 1984); and (3) alternative reproductive behaviors (Austad and Howard, 1984).

Acknowledgements

This study was funded by Federal Aid in Wildlife Restoration Projects W-21 and W-22. E. Crain, S. DuBois, L. Jennings, P. Karczmarczyk, T. McCall, L. McManus, C. Nuckols, W. Regelin, and D. Simpson helped in one or more aspects of field work. Visiting scientists, A. T. Bergerud and H. Butler, provided refreshing stimulation, obtained calving-related data in 1984, and directed us to pertinent literature. R. Cameron and K. Whitten critiqued the manuscript, and suggestions by them and reviewers D. Gauthier and R. Farnell improved the manuscript.

References

Austad, S. N., and **Howard, R. D.** 1984. Introduction to the symposium: alternative reproductive tactics. — *American Zoologist 24: 307 - 308.*

Bergerud, A. T. 1974*a*. The role of the environment in the aggregation, movement, and disturbance behavior of caribou. — *In: Geist, V., and Walther, F. (eds.). The behavior of ungulates and its relation to management. Volume 2. IUCN New Series Publication 24, Morges, Switzerland. 552 - 584.*

Bergerud, A. T. 1974*b*. Decline of caribou in North America following settlement. — *Journal of Wildlife Management 38: 757 - 770.*

Bergerud, A. T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. — *In: Reimers, E., Gaare, E., and Skjenneberg, S. (eds.). Proceedings of the Second International Reindeer/Caribou Symposium, Røros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 556 - 581.*

Bergerud, A. T. 1985. Antipredator strategies of caribou: dispersion along shorelines. — *Can. J. Zool. 63: 1324 - 1329.*

Bergerud, A. T., Butler, H. E., and **Miller, D. R.** 1984. Antipredator tactics of calving caribou: dispersion in mountains. — *Canadian Journal of Zoology 62: 1566 - 1575.*

Borowsky, B. 1985. Differences in reproductive behavior between two male morphs of the amphipod crustacean *Jassa folcata* Montagu. — *Physiological Zoology 58 (5): 497 - 502.*

Bunnell, F. L., and **Harestad, A. S.** 1983. Dispersal and dispersion of black-tailed deer: models and observations. —*Journal of Mammalogy 64 (2): 201 - 209.*

Davis, J. L. 1980. Status of *Rangifer* in the U.S.A. — *In: Reimers, E., Gaare E., and Skjenneberg, S. (eds.). Proceedings of the Second International Reindeer/ Caribou Symposium, Røros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 793 - 797.*

Davis, J. L. and **Valkenburg, P.** 1985. Demography of the Delta Caribou Herd under varying rates of natural mortality and harvest by humans. — *Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report Projects W-21-2, W-22-2, W-22-3, and W-22-4. Juneau, Alaska. 50 p.*

Edmonds, E. J., and **Bloomfield, M.** 1984. A study of woodland caribou *(Rangifer tarandus caribou)* in West Central Alberta, 1979 - 1983. — *Alberta Energy and Natural Resources, Fish and Wildlife Division. 203p. (Available Alberta Fish and Wildlife Division, 6909-116 Street, Edmonton.)*

Gauthier, D. A. 1984. Population limitation in the Burwash Caribou Herd, Southwest Yukon. — *Ph.D. Thesis. University of Waterloo. Waterloo, Ontario. 247 p.*

Gunn, A., and **Miller, F. L.** 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. — — *Rangifer, Special Issue No 1, 1986.*

Haber, G. C., and **Walters, C. J.** 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. — *In: Reimers, E., Gaare, E., and Skjenneberg, S. (eds.). Proceedings Second International Reindeer/Caribou Symposium, Røros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 645 - 663.*

Iwanaga, K., Tojo, S., and **Nagata, T.** 1985. Immigration of the brown planthopper, *Nilaparvata lugens,* exhibiting various responses to density in relation to wing morphism. — *Entomologia experimentalis et applicata 38 (2): 101 - 108.*

Jurss, K., Bittorf, T., Volker, T., Wacke, R., and **Bastrop, R.** 1985. Experimental studies of biochemical and physiological differences between the 3 morphs of the 3-spined stickleback, *Gasterosterus aculeatus* L. 3. Liver-somatic index and enzyme activities at different times of the year. — *Zoologische Jahrbücher 89 (4): 441 - 452.*

Klein, D. R., and **White, R. G.** 1978. Parameters of caribou population ecology in Alaska. — *Proceedings of Symposium and Workshop, Biological Papers of University of Alaska, Special Report No. 3. 49 p.*

Lent, P. C. 1965. Rutting behavior in a barren-ground caribou population. — *Animal Behavior 13: 259 - 264.*

Lott, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. — *Behaviour 88 (3 - 4): 266 - 325.*

Martell, A. E., and **Russell, D. E.** (eds.) 1985. Caribou and human activity. — *Proceedings First North American Caribou Workshop, Whitehorse, Yukon, 28 - 29 September 1983. Canadian Wildlife Service Special Publication, Ottawa. 68 p.*

Miller, F. L. 1974. Biology of the Kaminuriak population of barren-ground caribou. Part 2: Dentition as an indicator of age and sex; composition and socialization of the population. — *Canadian Wildlife Service Report Series No. 31. Queen's Printer, Ottawa. 88 p.*

Miller, F. L. 1982. Caribou *(Rangifer tarandus).* — *In: Chapman, J. A., and Feldhamer, G. A. (eds.). Wild Mammals of North America: biology, management, and economics. The Johns Hopkins University Press, Baltimore. 923 - 959.*

Parker, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part 1: Total numbers, mortality, recruitment and seasonal distribution. — *Canadian Wildlife Service Report Series No. 20. Queen's Printer, Ottawa. 95 p.*

Pegau, R. E. 1985. Caribou Survey-Inventory Progress Report: GMU 19 and 21. — *In: Seward, A. (ed.). Caribou Survey-Inventory Progress Report. Vol. XVI. Federal Aid in Wildlife Restoration Project W-22-4. 29 - 31.*

Ratti, T. T. 1985. A test of water depth niche partitioning by Western Grebe color morphs. — *Auk 102 (3): 635 - 636.*

Skoog, R. O. 1968. Ecology of the caribou *(Rangifer tarandus granti)* in Alaska. — *Ph. D. Thesis, University of California, Berkeley. 699 p.*

Thomas , D. C., Parker, G. R., Kelsall, J. P., and **Loughrey, A. G.** 1968. Population estimates of barren-ground caribou on the Canadian mainland from 1955 to 1967. — *Canadian Wildlife Service Progress Note No. 3. Ottawa. 5 p.*

Troyer, W. 1981. Movements of the Denali Caribou Herd. — *National Park Service. Anchorage, Alaska. 19 p. (Available from National Park Service, 2525 Gambell Street, Anchorage, 99703.)*

Valkenburg, P., and **Davis, J. L.** 1986. Calving distribution of Alaska's Steese-Fortymile Herd: A case of infidelity? — *Rangifer, Special Issue No 1, 1986.*