

The Canadian Field-Naturalist

A tribute to Arthur T. Bergerud, 1930–2019

BRIAN E. MCLAREN^{1,*}, HEATHER BUTLER², and RICK PAGE³

¹Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1 Canada

²1233 Isabella Point Road, Salt Spring Island, British Columbia V8K 1T5 Canada

³11810 Fairtide Road, Ladysmith, British Columbia V9G 1K5 Canada

*Corresponding author: bmclaren@lakeheadu.ca

McLaren, B.E., H. Butler, and R. Page. 2021. A tribute to Arthur T. Bergerud, 1930–2019. *Canadian Field-Naturalist* 135(1): 68–77. <https://doi.org/10.22621/cfn.v135i1.2813>

Dr. Arthur T. (Tom) Bergerud (Figure 1), aged 89, passed away on 27 November 2019. He left us to mourn the loss of the “Caribou biologist” who was also a provocative thinker on animal behaviour and population dynamics in wildlife, an activist for the specific causes he knew needed to be heard, and a respected professional to those who were blessed with time to get to know him as naturalist, scholar, peer, friend, and mentor. Tom was born on 11 November 1930 in Minneapolis, Minnesota, to Alf and Marjorie Bergerud. Alf was a lawyer and popular state politician for 30 years, and General Counsel and President of the midwestern grocery store chain, Red Owl. At its peak, the Red Owl chain had over 400 stores. Alf served a week shy of 11 000 days in public office.

Tom found little of interest in his father’s pursuits, instead spending much of his youth in outdoor adventures. Always enamoured of nature, Tom recounted to many the story of his first visit to the Bell Museum of Natural History on the St. Paul campus of the University of Minnesota. There, he saw a diorama depicting a cranberry bog on the Red Lake Peatland, about 100 km south of the Manitoba–Ontario border; the diorama featured taxidermy mounts of among the last Caribou (*Rangifer tarandus*) seen alive from this location in the state of Minnesota (Figure 2). It was on seeing this magnificent display that Tom convinced himself to be that “Caribou biologist” who could fight for the conservation of the species so emblematic of the boreal forest and much of the tundra of Canada and Alaska.

Tom’s academic and professional career started in 1953 with a B.Sc. in Wildlife Management from Oregon State University, after which he began work as a Fish and Wildlife Specialist at the Delta Waterfowl Research Station in Minnedosa, Manitoba. His friendship there with Hans Albert (Al) Hochbaum

almost led to M.Sc. research on ducks, but Tom knew that his two years of U.S. Army service was imminent, so this plan was put aside. After his army service, Tom was hired in 1956 as a District Wildlife Biologist in St. John’s, Newfoundland and Labrador, and by 1960 became Director of the Province’s Game Division.

While in Newfoundland and Labrador, Tom became familiar with parts of Canada that always remained dear to him. He published well into the

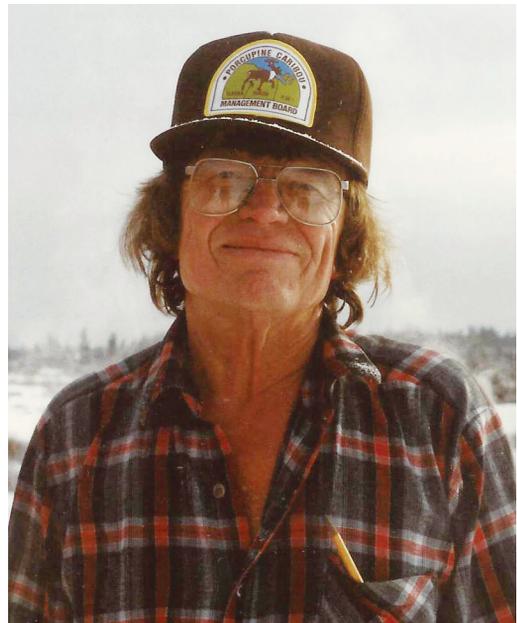


FIGURE 1. Arthur T. (Tom) Bergerud, 1930–2019. Photograph taken near the Kluane Lake Research Station *en route* to the Third North American Caribou Workshop held in Chena Hot Springs, Alaska, in November 1987. Photo: H. Butler.



FIGURE 2. Woodland Caribou (*Rangifer tarandus*) diorama in the original Bell Museum of Natural History, St. Paul, Minnesota, with famed painted backdrops by Francis Lee Jaques, ca. 1940. The diorama was viewed by visitors until renovation of the museum in 2016. Photo: P. Carroll, Wikimedia Commons.

1970s on some of the basics in monitoring Caribou and on the unique Caribou dynamics on the island of Newfoundland. Tom also used this time to embark on an M.Sc. degree in Wildlife Management from the University of Wisconsin in Madison (Bergerud 1961a) and a Ph.D. degree from the University of British Columbia (Bergerud 1969a). By 1971 he had published a summary on what he knew about Caribou in Newfoundland in No. 25 of the widely read *Wildlife Monograph* series (Bergerud 1971a). During this first part of his career, Tom also found time to help raise his first young children who all experienced rural life on the Avalon Peninsula.

Tom's publishing career spanned seven decades and over 100 published papers, and in the weeks before his passing, he did not arrest his passion for science. He could be found working on improvements to an earlier draft of his last manuscript, which documents the demise of the Caribou population on the Slate Islands, Ontario. It was published in the previous issue of *The Canadian Field-Naturalist* (Bergerud *et al.* 2020) and completes a part of Tom's career that started in the early 1970s, testing his hypothesis that Caribou in North America are limited by Gray Wolf (*Canis lupus*) predation (Bergerud 1974a). Regrettably, illustration of this hypothesis along the north shore of Lake Superior includes the near extirpation of Caribou from this part of their range, even in protected areas like Pukaskwa National Park (Bergerud *et al.* 2014). Tom made early alarm calls for this region (Bergerud *et al.* 2007), and pleas for wolf manage-

ment in many other areas where Caribou were threatened (Bergerud 2007).

Tom assisted wildlife conservation and management in Newfoundland and Labrador's pioneering years far beyond the work on Caribou in Newfoundland, by conducting research on Caribou in Labrador (Bergerud 1967a), and on Willow Ptarmigan (*Lagopus lagopus*; Bergerud and Mercer 1966, 1972; Bergerud and Huxter 1969a,b; Bergerud 1970a,b, 1971c, 1972a), Arctic Hare (*Lepus arcticus*; Bergerud 1967b), Moose (*Alces americanus*; Bergerud *et al.* 1962, 1968; Bergerud and Manuel 1969), American Marten (*Martes americana*; Bergerud 1969b), and American Beaver (*Castor canadensis*; Bergerud and Miller 1977) in Newfoundland. His last paper specific to Newfoundland (Bergerud 1983a) popularized in *Scientific American* the story of a unique predator, Canada Lynx (*Lynx canadensis*), which contributed to Caribou calf mortality at levels that could account for population decline in a 'simple ecosystem' driven by declines in Snowshoe Hare (*Lepus americanus*). The beauty of that paper was in demonstrating the role of prey switching.

Perhaps it was his use of the word "simple" in the title of the *Scientific American* paper that set Tom up for later criticism. It was almost two decades later that Coyotes (*Canis latrans*) became established in Newfoundland and played the role of the Gray Wolf in increasing calf mortality, as well as raising the vulnerability of Caribou in this part of the world. Tom's hypothesis of the predator's role for Caribou decline

was illustrated once again, this time by a new set of researchers who confirmed not just the likelihood of Tom's hypothesis involving canids, but also the importance of the bear and lynx as sources of calf mortality in Caribou (Mahoney *et al.* 2016; Lewis *et al.* 2017). Tom's tradition for good wildlife research in Newfoundland and Labrador continues.

Tom knew of the two main controversial elements to his career, and stick-handled them well. The first came with his publication of a paper with a title that named Caribou "buffalo of the North" (Bergerud *et al.* 1984b), a reference to their vulnerability to overharvest or poaching that can push a species to extirpation, like what happened earlier to Bison (*Bison bison*). The 1984 paper was motivated by the need for responsible construction of pipelines and highways in the north of Canada, in part to reduce access by hunters, but also by concerns about logging and other developments in the south of Canada. It was in this paper that the idea first surfaced that higher alternate prey abundance and subsequent high wolf densities in the southern and more disturbed portion of British Columbia (BC) were the proximate cause for Caribou declines. Tom recognized that logging *per se* was not detrimental but that it led to a cascade of changes in interactions with Caribou and their predators. Logging increased access by wolves and humans, increased density of predators with increases in alternate prey, and reduced the area of large predator-free habitat refuges for Caribou calving.

The "buffalo of the North" paper, published in *Arctic*, came at a controversial time in Canadian history, when the repercussions of Justice Thomas Berger's report on the potential effects of developing the Mackenzie Valley pipeline were resounding in the media. Bergerud *et al.* (1984b) twice cautioned about interpreting correlations of events in the population dynamics of Caribou as causes for effects. In addition, the authors attest agreement with the warning by C.C. Shank (1979, of the Arctic Institute of North America, University of Calgary, who wrote one of the industry-led reviews of effects of pipelines on northern mammals, as cited in Bergerud *et al.* 1984b: 8) that:

there is a potentially infinite universe of manners in which human activity can influence animal populations and merely demonstrating that one factor is not operative does not negate the influence of the remainder of possible factors.

Nevertheless, the sweeping review that encompassed Tom's experience with Caribou and their conservation at this time led some critics to believe that he and his co-authors (1) surrendered themselves to industry, (2) disregarded the potential that individual effects of disturbance on Caribou may translate to cause-and-effect relationships at the population level,

(3) filled their paper with inaccuracies in citation and omission of examples of documented effects of disturbance on *Rangifer tarandus*—for some reason, largely on Reindeer in Eurasia—and (4) referenced the literature selectively to make their points. These charges, in the form of letters to the Editor of *Arctic*, were humbly corrected by Bergerud *et al.* (1984c) and not so humbly confronted by Bergerud and Jakimchuk (1985). In the second response, Tom and consulting biologist Ronald Jakimchuk dryly extolled the virtues of Tom's having established 18 new Caribou populations, and of his helping to illustrate, largely in Newfoundland, that curtailing of regulated and unregulated hunting can restore Caribou populations. We suggest that a call for curtailing overharvest from all sources was the ultimate purpose of the Bergerud *et al.* (1984b) paper.

The second controversy arose a year later, when Tom and BC Ministry of Environment biologist John Elliott co-wrote the most memorable paper in Tom's bibliography (Bergerud and Elliott 1986). In it, they reviewed Caribou populations in northwestern BC, using reports of provincial biologists over approximately six decades on the harvest of Gray Wolves, Moose, and Caribou, including a period during 1949–1962 when wolves were controlled not only by bounty, but also by poisoned bait. They reviewed Gray Wolf and Caribou census data collected during their own experimental wolf control measures in 1977–1982 on one of the populations and compared to other areas without wolf control. The outcome matched Bergerud's (1974a) hypothesis on wolves limiting Caribou, although the work was criticized for rather coarse measures of demographics that spanned so many decades. What was undeniable was that during the experimental wolf control, populations increased predictably by 6% per year when no such increases occurred for the adjacent reference populations.

Figure 10 in Bergerud and Elliott (1986) increased the scope of the five Caribou populations it described to an additional 17 populations where Caribou calf counts were previously published, plus an additional 13 populations where Caribou mortality was estimated, in eight cases by some of the first radiocollared Caribou studies. Drawing on work from 1968 to 1985 in Caribou populations spanning Alaska and Canada, where Gray Wolf densities were also estimated, Bergerud and Elliott (1986) showed—Tom's graphics were always comprehensive—that mortality balanced recruitment at a point corresponding to 12% calves in a survey. This point matched a threshold density of 6.5 wolves per 1000 km². The figure was reproduced at the beginning of Tom's "open letter" written 20 years later and calling for management of

wolves as an urgent conservation measure (Bergerud *et al.* 2007); it is still frequently referenced by those urging for or implementing wolf control.

Part of what made Bergerud and Elliott's (1986) paper so elegant was how they showed that the expansion of Moose southward and westward in BC was correlated with increases in the threshold density of wolves that then corresponded to periods of Caribou decline. Moose were bigger prey at higher densities and could support more wolves than Caribou alone. The argument, while not a 'smoking gun', was a hypothesis on an indirect interaction between Moose and Caribou, mediated by their common predator, and based in Robert Holt's (1977) idea that 'apparent competition' could structure ecological communities. Indeed, there was cause for less controversy: calls for management of wolves could include reducing populations of Moose or other ungulates more abundant than Caribou, an argument that could be inferred from Bergerud and Elliott's (1998) second paper reviewing a similar geography in BC. Apparent competition was later identified by Tom, and accepted by most biologists, as a driver in the evolution of Boreal populations of Caribou; Tom adopted "rareness as an antipredator strategy to reduce predation risk" as a defining phrase for this ecotype in the title of his chapter in the *Wildlife 2001* series (Bergerud 1992).

What was controversial in Bergerud and Elliott's (1986) paper was that it supported wolf control. Tom later described wolf predation as the driver in Caribou evolution (Bergerud 1996), and the suggestion that predation by Gray Wolves could be the deciding factor in the decline of Caribou populations was not well received. Some readers found it alarming that 'top-down' effects could be so easily described in wildlife research. Tom caused disbelief in some other readers by further describing Caribou, where limited by food supply, as on the Slate Islands, Ontario, to be conforming to a "maintenance phenotype", a term coined by Valerius Geist (1998, in his book on deer evolution, as cited by Bergerud *et al.* 2007). It took time for biologists who previously had almost universally thought that food limitation was the driver of Caribou population dynamics to accept the norm of top-down control by wolves in most of Caribou range. Wolf control can immediately 'buy time', before other Caribou conservation measures, such as habitat restoration, take effect (Hervieux *et al.* 2015). But as Mech (2012) has pointed out, too many biologists wish to paint the wolf as a 'saint'.

Despite later support from Seip (1992) and Wittmer *et al.* (2005) from radio-tracking data on Caribou in southern BC, and despite continued tests of the hypothesis that declines in Caribou in northern BC were due to top-down control by wolves and appar-

ent competition (Serrouya *et al.* 2019), Bergerud's (1974a) and Bergerud and Elliott's (1986) hypotheses remain controversial to this day. The recent work of Serrouya *et al.* (2019) in BC and Alberta received the same sort of criticism about data precision that Tom often experienced (Harding *et al.* 2020); similarly, the work by Wittmer *et al.* (2005) received charges of methodological limitations (Brown *et al.* 2007). Ultimately, the criticism arises because a 'smoking gun' is difficult to find to justify cause-and-effect in ecology (Boertje *et al.* 2017).

The smoking gun is elusive for the ecological complexities that Tom in fact knew well. The examples involving Caribou declines that Tom witnessed and acknowledged include complexities not only in bear and lynx as additional predators in Newfoundland (Lewis *et al.* 2017), but also in variable effects of predation in Newfoundland that depend on weather (Bastille-Rousseau *et al.* 2015), on Caribou population dynamics (Mahoney *et al.* 2016), and on changes to their behaviour with food limitation (Schaefer *et al.* 2016). Variable Caribou population dynamics also occur with changing snow and freezing rain conditions in Labrador (Schmeltzer *et al.* 2020) and, as shown for the mountain populations in Alberta and BC, with human disturbance that can shift both Caribou behaviour (MacNearney *et al.* 2016) and Gray Wolf hunting efficiency (Pigeon *et al.* 2020). Caribou are also often not given enough space, and the space they are given as "critical habitat" continues to be fragmented; Palm *et al.* (2020) recently reiterated this point for the BC populations that were so often top of Tom's mind: fragmentation reduces or eliminates the value of the shrinking space for Caribou as a refuge from predation.

There is much irony in the fact that Tom listed the potential, and very often acknowledged the reality, of every one of the other contributing factors to Caribou decline listed above, yet could never completely win the argument for predation as the driving factor in shaping the behaviour of Caribou, and wolf control as a likely opportunity for Caribou rescue. Just one example to support Tom's case of careful consideration of multiple factors comes from his observations of the George River Caribou on the Ungava Peninsula (Bergerud and Luttich 2003). Indeed, in their book, *The Return of the Caribou to Ungava*, Bergerud *et al.* (2007) made the argument that limitations to the abundance of the George River population were due to nutritional effects caused by overgrazing of limited summer range, i.e., bottom-up and not top-down structuring of the ecosystem. Layne Adams (2009: 166) called Bergerud *et al.*'s (2007) work "an important reference for those interested in *Rangifer* populations throughout the world and ... for anyone

interested in ungulate ecology or northern ecosystems". Ironies aside, there is much sadness in the very large number of Caribou declines themselves.

Part of the success in Tom's career as a naturalist and biologist is owing to the alliances he made with steadfast colleagues and field personnel, in particular people who excelled in their own right. The collaboration with John Elliott co-occurred with an important study on Caribou calf mortality by R.P., at the time another BC biologist. Earlier, Newfoundland and Labrador biologist W.E. (Gene) Mercer collaborated with Tom on Caribou (Bergerud and Mercer 1968, 1989) and Willow Ptarmigan (Bergerud and Mercer 1966, 1972); later, biologist Stu (S.N.) Luttich, of the same provincial Wildlife Division, co-wrote *The Return of the Caribou to Ungava* (Bergerud *et al.* 2007) with Lo Camps, another long-time collaborator. A special kind of alliance in Newfoundland and Labrador was with two of this province's Conservation Officers, Mike (M.J.) Nolan (Bergerud *et al.* 1968; Bergerud and Nolan 1970) and Lloyd (L.R.) Russell (Bergerud *et al.* 1964; Bergerud and Russell 1964, 1966). These officers are among the most celebrated people throughout the province's Wildlife Division, and a credit to Newfoundland and Labrador's continued and unique recognition of Conservation Officers not just as enforcers of the law, but also as active participants in supporting research, should they choose this route. In the case of Mike Nolan, his recognition that poaching was a foremost barrier to recovery of the Avalon Caribou population, an idea that Tom helped reinforce, earned him an Honorary Doctor of Philosophy from Memorial University. The recognition was specific to his on-the-ground recovery efforts of the Avalon Caribou, efforts that Tom so kindly extolled (Figure 3), efforts that took this herd from a few hundred remaining individuals to a few thousand in three decades.

Throughout all the studies since 1974, Tom was accompanied and assisted by his wife, Heather Butler, who is also a biologist studying Caribou behaviour. Dave Mossop of Yukon College in Yellowknife and the late Michael Gratson assisted Tom in many studies on grouse. In Ontario, Tom's work on the Slate Islands and in Pukaskwa was assisted by many biologists, including Lo Camps from Salt Spring Island, but also Thunder Bay based H.R. (Tim) Timmermann, Terrace Bay District Biologist Barry Snider, Roger Ferguson also from Terrace Bay, Wawa based Gord Eason, and Sault Ste. Marie based W. (Bill) Dalton. Bill would be ready for any task on the Slate Islands, even though the trip was several hours away. He helped collect countless bones and antlers from deceased Caribou for Tom and Heather to return to Salt Spring Island, where Tom resided through most



FIGURE 3. Woodland Caribou (*Rangifer tarandus*) calf held by Tom Bergerud in Newfoundland. Photo: source and date unknown.

of his career. Gord's favourite story was Tom calling from a pay phone on the highway after he had just seen a Caribou and thought a local biologist should know about it because it was one that had been translocated to Lake Superior Provincial Park and had now moved south. Tom was not much for long phone calls, so Gord managed to say, "Yes, Tom, you just saw the southernmost mainland Caribou in the world". Tom replied "Okay, bye".

Literature Cited

(for publications by Bergerud cited above see Bibliography)

- Adams, L.G. 2009. Book Review: The return of caribou to Ungava (A.T. Bergerud, S.N. Luttich, and L. Camps. McGill-Queen's University Press, Montréal, Quebec, 2008, 586 pages). *Journal of Wildlife Management* 73: 165–166. <https://doi.org/10.2193/2008-380>
- Bastille-Rousseau, G., J.A. Schaefer, K.P. Lewis, M.A. Mumma, E.H. Ellington, N.D. Rayl, S.P. Mahoney, D. Pouliot, and D.L. Murray. 2015. Phase-dependent climate–predator interactions explain three decades of variation in neonatal caribou survival. *Journal of Animal Ecology* 85: 445–456. <https://doi.org/10.1111/1365-2656.12466>
- Boertje, R.D., C.L. Gardner, M.M. Ellis, T.W. Bentzen,

- and J.A. Gross. 2017. Demography of an increasing caribou herd with restricted wolf control. *Journal of Wildlife Management* 81: 429–448. <https://doi.org/10.1002/jwmg.21209>
- Brown, G.S., L. Landriault, D.J.H. Sleep, and F.F. Malory. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Oecologia* 154: 485–492. <https://doi.org/10.1007/s00442-007-0855-3>
- Harding, L.E., M. Bourbonnais, A.T. Cook, T. Spribille, V. Wagner, and C. Darimont. 2020. No statistical support for wolf control and maternal penning as conservation measures for endangered mountain caribou. *Biodiversity and Conservation* 29: 3051–3060. <https://doi.org/10.1007/s10531-020-02008-3>
- Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2015. Addendum to “Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta.” *Canadian Journal of Zoology* 93: 245–247. <https://doi.org/10.1139/cjz-2015-0012>
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197–229. [https://doi.org/10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9)
- Lewis, K.P., S.E. Gullage, D.A. Fifield, D.H. Jennings, and S.P. Mahoney. 2017. Manipulations of black bear and coyote affect caribou calf survival. *Journal of Wildlife Management* 81: 122–132. <https://doi.org/10.1002/jwmg.21174>
- MacNearney, D., K. Pigeon, G. Stenhouse, W. Nijland, N.C. Coops, and L. Finnegan. 2016. Heading for the hills? Evaluating spatial distribution of woodland caribou in response to a growing anthropogenic disturbance footprint. *Ecology and Evolution* 6: 6484–6509. <https://doi.org/10.1002/ece3.2362>
- Mahoney, S.P., K.P. Lewis, J.N. Weir, S.F. Morrison, J.G. Luther, J.A. Schaefer, D. Pouliot, and R. Lati-fovic. 2016. Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study. *Population Ecology* 58: 91–103. <https://doi.org/10.1007/s10144-015-0525-y>
- Mech, D.L. 2012. Is science in danger of sanctifying the wolf? *Biological Conservation* 150: 143–149. <https://doi.org/10.1016/j.biocon.2012.03.003>
- Palm, E.C., S. Fluker, H.K. Nesbitt, A.L. Jacob, and M. Hebblewhite. 2020. The long road to protecting critical habitat for species at risk: the case of southern mountain woodland caribou. *Conservation Science and Practice* 2: e219. <https://doi.org/10.1111/csp.2.219>
- Pigeon, K.E., D. MacNearney, M. Hebblewhite, M. Musiani, L. Neufeld, J. Cranston, G. Stenhouse, F. Schmiegelow, and L. Finnegan. 2020. The density of anthropogenic features explains seasonal and behaviour-based functional responses in selection of linear features by a social predator. *Scientific Reports* 10: 11437. <https://doi.org/10.1038/s41598-020-68151-7>
- Schaefer, J.A., S.P. Mahoney, J.N. Weir, J.G. Luther, and C.E. Soulliere. 2016. Decades of habitat use reveal food limitation of Newfoundland caribou. *Journal of Mammalogy* 97: 386–393. <https://doi.org/10.1093/jmammal/gyv184>
- Schmeltzer, I., K.P. Lewis, J.D. Jacobs, and S.C. McCarthy. 2020. Boreal caribou survival in a warming climate, Labrador, Canada 1996–2014. *Global Ecology and Conservation* 23: e01038. <https://doi.org/10.1016/j.gecco.2020.e01038>
- Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70: 1494–1503. <https://doi.org/10.1139/z92-206>
- Serrouya, R., D.R. Seip, D. Hervieux, B.N. McLellan, R.S. McNay, R. Steenweg, D.C. Heard, M. Hebblewhite, M. Gillingham, and S. Boutin. 2019. Saving endangered species using adaptive management. *Proceedings of the National Academy of Sciences* 116: 6181–6186. <https://doi.org/10.1073/pnas.1816923116>
- Wittmer, H.U., A.R.E. Sinclair, and B.N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144: 257–267. <https://doi.org/10.1007/s00442-005-0055-y>

Bibliography

- Bergerud, A.T. 1958. Distribution, movement, and population dynamics of Newfoundland caribou March 1957 to March 1958. *Canadian Wildlife Service Report No. 925*, Ottawa, Ontario, Canada.
- Bergerud, A.T. 1959. Book Review: *The new way of the wilderness* (C. Rutstrum. The Macmillan Co., New York, 1958, 276 pages). *Journal of Wildlife Management* 23: 248–249. <https://doi.org/10.2307/3797662>
- Bergerud, A.T. 1961a. Reproduction of Newfoundland caribou. M.Sc. thesis, University of Wisconsin, Madison, Wisconsin, USA.
- Bergerud, A.T. 1961b. Sex determination of caribou calves. *Journal of Wildlife Management* 25: 205. <https://doi.org/10.2307/3798682>
- Bergerud, A.T. 1962. Ten years of wildlife research in Newfoundland. Pages 17–38 in *1961 Wildlife Management Papers, 25th Federal-Provincial Wildlife Conference*. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Bergerud, A.T., F. Manuel, and H. Whalen. 1962. Moose management studies in Central Newfoundland. *Proceedings, Northeast Wildlife Conference*, Monticello, New York, USA.
- Bergerud, A.T. 1963. Aerial winter census of caribou. *Journal of Wildlife Management* 27: 438–449. <https://doi.org/10.2307/3798518>
- Bergerud, A.T., S.S. Peters, and R. McGrath. 1963. Determining sex and age of willow ptarmigan in Newfoundland. *Journal of Wildlife Management* 27: 700–711. <https://doi.org/10.2307/3798486>

- Bergerud, A.T.** 1964a. Relationship of mandible length to sex in Newfoundland caribou. *Journal of Wildlife Management* 28: 54–56. <https://doi.org/10.2307/3797936>
- Bergerud, A.T.** 1964b. A field method to determine annual parturition rates for Newfoundland caribou. *Journal of Wildlife Management* 28: 477–480. <https://doi.org/10.2307/3798200>
- Bergerud, A.T., A. Butt, H.L. Russell, and H. Whalen.** 1964. Immobilization of Newfoundland caribou and moose with succinylcholine chloride and Cap-Chur equipment. *Journal of Wildlife Management* 28: 49–53. <https://doi.org/10.2307/3797935>
- Bergerud, A.T., and H.L. Russell.** 1964. Evaluation of rumen food analysis for Newfoundland caribou. *Journal of Wildlife Management* 28: 809–814. <https://doi.org/10.2307/3798798>
- Bergerud, A.T., and W.E. Mercer.** 1966. Census of willow ptarmigan in south-eastern Newfoundland. *Journal of Wildlife Management* 30: 101–113. <https://doi.org/10.2307/3797889>
- Bergerud, A.T., and H.L. Russell.** 1966. Extraction of incisors of Newfoundland caribou. *Journal of Wildlife Management* 30: 842–843. <https://doi.org/10.2307/3798294>
- Bergerud, A.T.** 1967a. Management of Labrador caribou. *Journal of Wildlife Management* 31: 621–642. <https://doi.org/10.2307/3797966>
- Bergerud, A.T.** 1967b. The distribution and abundance of Arctic Hares in Newfoundland. *Canadian Field-Naturalist* 81: 242–248. Accessed 10 November 2020. <https://www.biodiversitylibrary.org/page/28370926>.
- Bergerud, A.T., and F. Manuel.** 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. *Journal of Wildlife Management* 32: 729–746. <https://doi.org/10.2307/3799547>
- Bergerud, A.T., F. Manuel, and H. Whalen.** 1968. Harvest reduction of a moose population in Newfoundland. *Journal of Wildlife Management* 32: 722–728. <https://doi.org/10.2307/3799546>
- Bergerud, A.T.** 1969a. The population dynamics of Newfoundland caribou. Ph.D. thesis, University of British Columbia, Vancouver, British Columbia, Canada. <https://doi.org/10.14288/1.0104108>
- Bergerud, A.T.** 1969b. The status of Pine Marten in Newfoundland. *Canadian Field-Naturalist* 83: 128–131. Accessed 10 November 2020. <https://www.biodiversitylibrary.org/page/28060049>.
- Bergerud, A.T.** 1969c. Book Review: The caribou have returned (The migratory barren-ground caribou of Canada. Kelsall, J.P. Department of Indian Affairs and Northern Development, Canadian Wildlife Service, Ottawa, Ontario, Canada, 1968, 340 pages). *Ecology* 50: 940–941. <https://doi.org/10.2307/1933718>
- Bergerud, A.T.** 1969d. Numbers and densities. Pages 21–42 in *A Practical Guide to the Study of Productivity of Large Herbivores*. Edited by F.B. Golley and H.K. Buechner. Blackwell, Oxford, United Kingdom.
- Bergerud, A.T., and D.S. Huxter.** 1969a. Breeding season habitat utilization and movement of Newfoundland willow ptarmigan. *Journal of Wildlife Management* 47: 967–974. <https://doi.org/10.2307/3799333>
- Bergerud, A.T., and D.S. Huxter.** 1969b. Effects of hunting on willow ptarmigan in Newfoundland. *Journal of Wildlife Management* 47: 989–998. <https://doi.org/10.2307/3799318>
- Bergerud, A.T., and F. Manuel.** 1969. Aerial census of moose in central Newfoundland. *Journal of Wildlife Management* 33: 910–916. <https://doi.org/10.2307/3799324>
- Bergerud, A.T.** 1970a. Population dynamics of the willow ptarmigan *Lagopus lagopus alleni* L. in Newfoundland 1955 to 1965. *Oikos* 21: 299–325. <https://doi.org/10.2307/3543687>
- Bergerud, A.T.** 1970b. Vulnerability of willow ptarmigan to hunting. *Journal of Wildlife Management* 34: 282–285. <https://doi.org/10.2307/3799012>
- Bergerud, A.T.** 1970c. Eruption of permanent premolars and molars for Newfoundland caribou. *Journal of Wildlife Management* 34: 962–963. <https://doi.org/10.2307/3799172>
- Bergerud, A.T., and M.J. Nolan.** 1970. Food habits of hand-reared caribou *Rangifer tarandus* L. in Newfoundland. *Oikos* 21: 348–350. <https://doi.org/10.2307/3543694>
- Bergerud, A.T.** 1971a. The population dynamics of Newfoundland caribou. *Wildlife Monographs* 25: 3–55.
- Bergerud, A.T.** 1971b. The past abundance of Willow Ptarmigan on the Avalon Peninsula of Newfoundland. *Canadian Field-Naturalist* 85: 21–23. Accessed 1 March 2021. <https://www.biodiversitylibrary.org/page/28044440>.
- Bergerud, A.T.** 1971c. Hunting of stag caribou in Newfoundland. *Journal of Wildlife Management* 31: 71–75. <https://doi.org/10.2307/3799873>
- Bergerud, A.T.** 1971d. Abundance of forage on the winter range of Newfoundland caribou. *Canadian Field-Naturalist* 85: 39–52. Accessed 10 November 2020. <https://www.biodiversitylibrary.org/page/28044458>.
- Bergerud, A.T.** 1972a. Changes in the vulnerability of ptarmigan to hunting in Newfoundland. *Journal of Wildlife Management* 36: 104–109. <https://doi.org/10.2307/3799193>
- Bergerud, A.T.** 1972b. Food habits of Newfoundland caribou. *Journal of Wildlife Management* 36: 913–923. <https://doi.org/10.2307/3799448>
- Bergerud, A.T., and W.E. Mercer.** 1972. Spring foods of willow ptarmigan *Lagopus lagopus alleni* in south-eastern Newfoundland. *Oikos* 23:213–217. <https://doi.org/10.2307/3543408>
- Redfield, J.A., F.C. Zwickel, J.F. Bendell, and A.T. Bergerud.** 1972. Temporal and spatial patterns of allele and genotype frequencies at the *Ng* locus in blue grouse (*Dendragapus obscurus*). *Canadian Journal of Zoology* 50: 1657–1662. <https://doi.org/10.1139/z72-218>
- Bergerud, A.T.** 1973. Movement and rutting behaviour of Caribou (*Rangifer tarandus*) at Mount Albert, Quebec. *Canadian Field-Naturalist* 87: 357–367. Accessed 1 March 2021. <https://www.biodiversitylibrary.org/page/28059082>.
- Bergerud A.T.** 1974a. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38: 757–770. <https://doi.org/10.2307/3800042>
- Bergerud, A.T.** 1974b. Relative abundance of food in winter

- for Newfoundland caribou. *Oikos* 25: 379–387. <https://doi.org/10.2307/3543960>
- Bergerud, A.T.** 1974c. Rutting behaviour of Newfoundland caribou. Pages 395–435 in *The Behaviour of Ungulates and its Relation to Management*. Volume 1. *Edited by* V. Geist and F. Walther. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.
- Bergerud, A.T.** 1974d. The role of the environment in the aggregation, movement and disturbance of behaviour of caribou. Pages 552–584 in *The Behaviour of Ungulates and its Relation to Management*. Volume 2. *Edited by* V. Geist and F. Walther. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.
- Donaldson, J.L., and A.T. Bergerud.** 1974. Behaviour and habitat selection of an insular population of blue grouse. *Syesis* 7: 115–127.
- Barclay, H.J., and A.T. Bergerud.** 1975. Demography and behavioral ecology of California quail on Vancouver Island. *Condor* 77: 315–323. <https://doi.org/10.2307/1366227>
- Bergerud, A.T.** 1975. Reproductive season of Newfoundland caribou. *Canadian Journal of Zoology* 53: 1213–1221. <https://doi.org/10.1139/z75-145>
- Bergerud, A.T., and H.D. Hemus.** 1975. An experimental study of the behavior of blue grouse (*Dendragapus obscurus*). I. Differences between the founders from three populations. *Canadian Journal of Zoology* 53: 1222–1237. <https://doi.org/10.1139/z75-146>
- Bergerud, A.T.** 1976. The annual antler cycle in Newfoundland Caribou. *Canadian Field-Naturalist* 90: 449–463. Accessed 10 November 2020. <https://www.biodiversitylibrary.org/page/28045940>.
- Bergerud, A.T.** 1977. Diets for caribou. Pages 243–266 in *CRC Handbook Series on Nutrition and Food*. Section G, Volume 1. *Edited by* M. Rechcigl. CRC Press, Cleveland, Ohio, USA.
- Bergerud, A.T., and D.R. Miller.** 1977. Population dynamics of Newfoundland beaver. *Canadian Journal of Zoology* 55: 1480–1492. <https://doi.org/10.1139/z77-192>
- Bergerud, A.T.** 1978a. The status and management of caribou in British Columbia. Fish and Wildlife Branch report. British Columbia Ministry of Recreation and Conservation. Victoria, British Columbia, Canada.
- Bergerud, A.T.** 1978b. Caribou. Pages 83–101 in *Big Game of North America: Ecology and Management*. *Edited by* J.L. Schmidt and D.L. Gilbert. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bergerud, A.T., and H.E. Butler.** 1978. Life history studies of caribou in Spatsizi Wilderness Park 1977–1978. British Columbia Ministry of Recreation and Conservation, Parks Branch, Victoria, British Columbia, Canada.
- Butler, H.E., and A.T. Bergerud.** 1978. The unusual story of the Slate Islands caribou. *Nature Canada* 7: 37–40.
- Bergerud, A.T.** 1979. Access: greatest threat to caribou. *Western Guidelines* 11: 5–9.
- Bergerud, A.T.** 1980a. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556–581 in *Proceedings of the 1979 International Reindeer/Caribou Symposium, 1979*. *Edited by* E. Reimers, E. Gaare, and S. Skjenneg. Røros, Norway.
- Bergerud, A.T.** 1980b. Status of Rangifer in Canada: I. Woodland caribou (*Rangifer tarandus caribou*). Pages 748–753 in *Proceedings of the 1979 International Reindeer/Caribou Symposium, 1979*. *Edited by* E. Reimers, E. Gaare, and S. Skjenneg. Røros, Norway.
- Bergerud, A.T.** 1981. The decline of moose in Ontario - a different view. *Alces* 17: 30–43.
- Bergerud, A.T.** 1982. Caribou. Pages 268–270 in *Handbook of Census Methods for Terrestrial Vertebrates*. *Edited by* D.E. Davis. CRC Press, Boca Raton, Florida, USA.
- Bergerud, A.T.** 1983a. Prey switching in a simple ecosystem. *Scientific American* 249: 130–141.
- Bergerud, A.T.** 1983b. The natural population control of caribou. Pages 14–61 in *Symposium on Natural Regulation of Wildlife Populations*. *Edited by* F.L. Bunnell, D.S. Eastman, and J.M. Peek. Forest, Wildlife and Range Experimental Station, University of Idaho, Moscow, Idaho, USA.
- Bergerud, A.T., M.J. Nolan, K. Curnew, and W.E. Mercer.** 1983. Growth of the Avalon Peninsula, Newfoundland caribou herd. *Journal of Wildlife Management* 47: 989–998. <https://doi.org/10.2307/3808157>
- Bergerud, A.T., W. Wyatt, and B. Snider.** 1983. The role of wolf predation in limiting a moose population. *Journal of Wildlife Management* 47: 977–988. <https://doi.org/10.2307/3808156>
- Bergerud, A.T., H.E. Butler, and D.R. Miller.** 1984a. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62: 1566–1575. <https://doi.org/10.1139/z84-229>
- Bergerud, A.T., R.D. Jakimchuk, and D.R. Carruthers.** 1984b. The buffalo of the North: Caribou (*Rangifer tarandus*) and human developments. *Arctic* 37: 1–90. <https://doi.org/10.14430/arctic2158>
- Bergerud, A.T., R.D. Jakimchuk, and D.R. Carruthers.** 1984c. Letter to the editor. *Arctic* 37: 294–295. In response to K.R. Whitten and R.D. Cameron, 1984, Letter to the editor, *Arctic* 37: 293, and to D.R. Klein and R.G. White, 1984, Letter to the editor, *Arctic* 37: 293–294.
- Bergerud, A.T., and D.H. Mossop.** 1984. The pair bond in ptarmigan. *Canadian Journal of Zoology* 62: 2129–2141. <https://doi.org/10.1139/z84-309>
- Page, R.E., and A.T. Bergerud.** 1984. A genetic explanation for ten-year cycles of grouse. *Oecologia* 64: 54–60. <https://doi.org/10.1007/BF00377543>
- Bergerud, A.T.** 1985a. Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology* 63: 1324–1329. <https://doi.org/10.1139/z85-199>
- Bergerud, A.T.** 1985b. The additive effect of hunting mortality on the natural mortality rates of grouse. Pages 345–366 in *Game Harvest Management*. *Edited by* S.L. Beasom and S.F. Roberson. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, USA.
- Bergerud, A.T., and H.E. Butler.** 1985. Aggressive and spacing behavior of female blue grouse. *Auk* 102: 313–322. <https://doi.org/10.2307/4086774>
- Bergerud, A.T., and R.D. Jakimchuk.** 1985. Letter to the editor. *Arctic* 38: 155–156. In response to F.L. Miller and A. Gunn, Letter to the editor, *Arctic* 38: 154–155.

- Bergerud, A.T., D.H. Mossop, and S. Myrberger.** 1985. A critique of the mechanics of annual changes in ptarmigan numbers. *Canadian Journal of Zoology* 63: 2240–2248. <https://doi.org/10.1139/z85-332>
- Bergerud, A.T., and J.P. Elliott.** 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64: 1515–1529. <https://doi.org/10.1139/z86-226>
- Bergerud, A.T.** 1987. Reply to Watson and Moss (1987). *Canadian Journal of Zoology* 65: 1048–1050. <https://doi.org/10.1139/z87-167>
- Bergerud, A.T., and H.E. Butler.** 1987. Response to S.J. Hannon and F.C. Zwickel. *Auk* 104: 345–347. <https://doi.org/10.1093/auk/104.2.345>
- Bergerud, A.T., and R.E. Page.** 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology* 65: 1597–1606. <https://doi.org/10.1139/z87-249>
- Bergerud, A.T.** 1988a. Caribou, wolves and man. *Trends in Ecology & Evolution* 3: 6872. [https://doi.org/10.1016/0169-5347\(88\)90019-5](https://doi.org/10.1016/0169-5347(88)90019-5)
- Bergerud, A.T.** 1988b. Caribou declines in central and southern British Columbia. Pages 201–225 in *Caribou Research and Management in British Columbia. Proceedings of a Workshop.* Edited by R. Page. B.C. Ministry of Forests WHR-27. B.C. Ministry of Environment Wildlife Branch WR-41, Victoria, British Columbia, Canada.
- Bergerud, A.T.** 1988c. Demography and behavior of insular blue grouse populations. Pages 29–77 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T.** 1988d. Mating systems in grouse. Pages 439–472 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T.** 1988e. Population ecology of North American grouse. Pages 578–685 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T.** 1988f. Increasing the numbers of grouse. Pages 686–734 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T., and W.B. Ballard.** 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. *Journal of Wildlife Management* 52: 344–357. <https://doi.org/10.2307/3801247>
- Bergerud, A.T., and M.W. Gratson.** 1988a. Adaptive Strategies and Population Ecology of Northern Grouse. *Population Studies.* University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T., and M.W. Gratson.** 1988b. Survival and breeding strategies of grouse. Pages 473–577 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T., and J.B. Snider.** 1988. Predation in the dynamics of moose populations: a reply. *Journal of Wildlife Management* 52: 559–564. <https://doi.org/10.2307/3801611>
- Davies, R.G., and A.T. Bergerud.** 1988. Demography and Behavior of Ruffed Grouse in British Columbia. Pages 78–121 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Ferguson, S.H., A.T. Bergerud, and R. Ferguson.** 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* 76: 236–245. <https://doi.org/10.1007/BF00379957>
- Page, R.E., and A.T. Bergerud.** 1988. A genetic explanation for ten-year cycles of grouse. Pages 423–438 in *Adaptive Strategies and Population Ecology of Northern Grouse. Population Studies.* Edited by A.T. Bergerud and M.W. Gratson. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Bergerud, A.T., and W.B. Ballard.** 1989. Wolf predation on the Nelchina caribou herd: a reply. *Journal of Wildlife Management* 53: 251–259. <https://doi.org/10.2307/3801343>
- Bergerud, A.T., and W.E. Mercer.** 1989. Caribou introductions in eastern North America. *Wildlife Society Bulletin* 17: 111–120.
- Bergerud, A.T., R. Ferguson, and H.E. Butler.** 1990. Spring migration and dispersion of woodland caribou calving. *Animal Behaviour* 39: 360–368. [https://doi.org/10.1016/S0003-3472\(05\)80882-6](https://doi.org/10.1016/S0003-3472(05)80882-6)
- Gratson, M.W., G.K. Gratson, and A.T. Bergerud.** 1991. Male dominance and copulation disruption do not explain variance in male mating success on sharp-tailed grouse (*Tympanuchus phasianellus*) leks. *Behaviour* 118: 187–213. <https://doi.org/10.1163/156853991X00283>
- Røed, K.H., M.A.D. Ferguson, M. Crête, and A.T. Bergerud.** 1991. Genetic variation in transferrin as a predictor for differentiation and evolution of caribou from eastern Canada. *Rangifer* 11: 65–74. <https://doi.org/10.7557/2.11.2.979>
- Bergerud, A.T.** 1992. Rareness as an antipredator strategy to reduce predation risk for moose and caribou. Pages 1008–1021 in *Wildlife 2001: Populations.* Edited by D.R. McCullough and R.H. Barrett. Elsevier Applied Science Publishers, London, United Kingdom, and New York, New York, USA. <https://doi.org/10.1007/978-94-011-2868-1>
- Bergerud, A.T.** 1996. Evolving perspectives on caribou dynamics, have we got it right yet? *Rangifer* 16: 95–115. <https://doi.org/10.7557/2.16.4.1225>
- Bergerud, A.T., and J.P. Elliott.** 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology* 76: 1551–1569. <https://doi.org/10.1139/z98-083>
- Bergerud, A.T.** 2000. Caribou. Pages 658–693 in *Ecology and Management of Large Mammals in North America.*

- Edited by* S. Demarais and P.R. Krausmann. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Bergerud, A.T., and S.N. Luttich.** 2003. Predation risk and optimal foraging trade-off in the demography and spacing of the George River herd, 1958 to 1993. *Rangifer* 23: 163–191. <https://doi.org/10.7557/2.23.5.1699>
- Bergerud, A.T.** 2007. The need for the management of wolves — an open letter. *Rangifer* 27: 39–50. <https://doi.org/10.7557/2.27.4.319>
- Bergerud, A.T., W.J. Dalton, H.E. Butler, L. Camps, and R. Ferguson.** 2007. Woodland caribou persistence and extirpation in relic populations on Lake Superior. *Rangifer* 27: 57–78. <https://doi.org/10.7557/2.27.4.321>
- Bergerud, A.T., S.N. Luttich, and L. Camps.** 2007. The Return of Caribou to Ungava. McGill-Queen's University Press, Montreal, Quebec, Canada.
- Crichton, V., and A.T. Bergerud.** 2011. Moose. Canadian Encyclopedia Historica Canada. Accessed 10 November 2020. <https://www.thecanadianencyclopedia.ca/en/article/moose>.
- Bergerud, A.T.** 2012. Caribou. Canadian Encyclopedia. Historica Canada. Accessed 10 November 2020. <https://www.thecanadianencyclopedia.ca/en/article/caribou>.
- Bergerud, A.T., B.E. McLaren, L. Krysl, K. Wade, and W. Wyett.** 2014. Losing the predator-prey space race leads to extirpation of woodland caribou from Pukaskwa National Park. *Ecoscience* 21: 374–386. [https://doi.org/10.2980/21-\(3-4\)-3700](https://doi.org/10.2980/21-(3-4)-3700)
- Bergerud, A.T., B.E. McLaren, W. Dalton, L. Camps, H.E. Butler, and R.S. Ferguson.** 2020. Changes to Caribou (*Rangifer tarandus*) in Slate Islands Provincial Park following successive arrivals of Gray Wolves (*Canis lupus*). *Canadian Field-Naturalist* 134: 342–352. <https://doi.org/10.22621/cfn.v134i4.1964>

Received 2 March 2021

Accepted 10 May 2021