# STUMBLING TOWARDS ENLIGHTENMENT: UNDERSTANDING CARIBOU DYNAMICS

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ABSTRACT: I review what biologists now think we know about caribou dynamics (Rangifer tarandus) and how we came by this knowledge, in the hope that there are some lessons that will help us learn more efficiently in the future. Prior to the late 1940s, most knowledge about caribou was obtained from anecdotal accounts of explorers, miners, government officials, and from the traditional knowledge of Native peoples. From the late 1940s to the early 1960s, there was a great leap forward due to the use of modern aircraft for wildlife surveys, the establishment of the wildlife management program at the University of Alaska, wolf (Canis lupus) control, and the increased availability of funding for wildlife research in Canada and Alaska. During the 1960s, particularly in Alaska, accumulation of knowledge slowed because of the change in administration from federal to state management, a shift in management and research priorities from caribou to moose (Alces alces), decreased funding and personnel for wildlife management, and because caribou were abundant throughout Alaska. Caribou were still viewed as a rather "unmanageable" species because of misunderstandings about population identity, population limitation and regulation, and caribou movements. Major declines in populations during the early 1970s, development of reliable radio collars, and much greater availability of affordable helicopters led to a renaissance in caribou research during the late 1970s. During the mid to late 1980s, new information accrued more slowly while most herds were increasing again. Widespread declines of caribou in the early 1990s, in conjunction with ongoing long-term research on population dynamics, weather, and predation, provided a large amount of new information. Knowledge about caribou dynamics, like the advancement of science, in general, has not come in a gradual way. There have been periods of stagnation when caribou populations were high, interspersed with periods of confusion, and then rapidly expanded research as herds declined. Despite greatly expanded knowledge, managers still have a limited ability to control caribou numbers, and the primary function of managers will continue to be providing for caribou hunting, while ensuring that hunting does not cause herds to decline to undesirably low levels. An increasingly important function for managers is providing accurate information to the public about caribou dynamics and the rationale for hunting regulations. Caribou biologists and managers should not be defensive or embarrassed about being wrong when new information casts doubt on old ideas, and creative new approaches to learning should be encouraged.

ALCES VOL. 37 (2): 457-474 (2001)

Keywords: aircraft, caribou herds, genetics, management, radio collars, Rangifer tarandus, research, traditional knowledge, University of Alaska Fairbanks, wolf control

Compared with what biologists knew about caribou dynamics (*Rangifer tarandus*) 25 years ago, we know much more today. There is still more to learn, however, and as a research biologist, I frequently ponder how we can most efficiently go about learning what we still need to know. Is there a way to hurry the accumulation of knowledge? Can we learn from the past? In this process, I think it is instructive to consider how we have accumulated knowledge about caribou dynamics and whether knowing this will help us more efficiently accumulate knowledge in the

future. In this paper, I review what we know or think we know about caribou dynamics and how we came by that knowledge. I also compare the development of knowledge about caribou with the advancement of scientific knowledge, in general (c.f. Romesburg 1981). This review is from the perspective of an Alaskan caribou biologist with experience from the last quarter of the 20<sup>th</sup> century, or what amounts to the last one-half of the period of modern caribou research, at least in North America. My perspective is also that of a research biologist for a management agency and I therefore have placed most emphasis on knowledge and research (basic or applied) that has had a direct effect on how we manage caribou. This paper is not intended to be a thorough historical review, but I have outlined what I consider to be major landmarks in the accumulation of knowledge of caribou in Alaska (Table 1). Many references are to events and discoveries from outside Alaska because of considerable research on caribou and reindeer that has taken place in Canada and Norway, respectively. I have considered arguments from colleagues and reviewers about the relative importance of various developments, technological advances, and historical events, and I have tried to be as objective as possible from my point of view.

#### Our Understanding of Caribou Dynamics Before the 1940s

Prior to the late 1940s, most information about caribou was largely descriptive and anecdotal (Skoog 1968, Burch 1999). Skoog (1968) thoroughly reviewed the historical literature on caribou in Alaska; most of that information came from the journals of explorers, travelers, early pioneers, and indirectly through the traditional knowledge of Native peoples. Caribou were viewed as a rather mysterious animal. The prevailing Inupiat view of caribou numbers and move-

ments was that these herbivores were unpredictable because they moved "around the world," and if they were scarce or absent for several years, people only had to wait and they would eventually return (S. Paniak, hunter, Anaktuvuk Pass, personal communication). Unusual events, such as large, unexpected movements of caribou near settlements were reported widely and remembered, whereas "normal" distribution and movements of caribou were seldom mentioned. In addition, much of what people wrote about caribou was speculative, and it is difficult for biologists reviewing older reports and orally quoted traditional knowledge to sort speculation from observation (c.f. Skoog 1968:217). As a result, much information on caribou before the 1940s was contradictory. Even in the few instances where trained biologists tried to estimate caribou numbers and describe herd movements objectively, their methods were severely constrained by the technology of the day (Murie 1935, Clarke 1940). For example, the 1920 estimate of 0.5-1 million caribou in the Fortymile Herd (then called Alaska-Yukon caribou) was based upon observation of only about 17,000 animals (Murie 1935).

#### Late 1940s and 1950s

Following World War II, the widespread availability of reliable "bush" planes (e.g., Noordyn Norseman, Piper Super Cub, DeHavilland Beaver, Grumman Goose, and Gull-wing Stinson) and the large number of war-trained pilots resulted in a boom in the use of aircraft for transportation and reconnaissance in the north. For the first time, aircraft were used to survey wildlife systematically (Scott et al. 1950, Banfield 1954, Skoog 1956, Siniff and Skoog 1964). The Canadian Wildlife Service and the U.S. Fish and Wildlife Service began systematic studies of caribou in the Northwest Territories and in Alaska in 1948 (Banfield 1954, Skoog

Event	Date	Contribution to development of knowledge and understanding of caribou
Crash of Western Arctic Herd (Burch 1999)	1880s	First good documentation that caribou numbers can change rapidly and cause extreme hardship for Native peoples.
Publication of Alaska-Yukon Caribou and Biological Investigation of the Thelon Game Sanctuary (Murie 1935, Clarke 1940)	1935, 1940	First scientific description of Alaskan caribou and historical review of their distribution in the state. Description of Fortymile Herd and its range. Beginning of modern research on caribou in Canada.
First systematic use of aircraft for wildlife surveys (Scott et al. 1950, Banfield 1954)	1 <b>94</b> 8	First aerial counts and documentation of range- wide distribution in Alaska and Northwest Territories.
Establishment of University of Alaska wildlife management program	1949 1950	Beginning of formal training of wildlife students and several caribou research projects. The University became a focal point for caribou research.
Widespread wolf control by the federal government in Alaska (Rausch 1967)	1950s	Caribou herds increased from low levels to become economically important once more. Wolf control can result in spectacular increases in caribou numbers.
Publication of A Revision of the Reindeer and Caribou, Genus Rangifer (Banfield 1961)	1961	First review of caribou classification, morphology, and archaeological data.
Project Chariot in northwestern Alaska (Lent 1966)	1959 -1962	Provided a large amount of money for research on caribou. Development of aerial photocensus techniques. Description of Western Arctic Herd and its range.
Eruption and crash of reindeer on St. Matthew Island (Klein 1968)	1955 1964	<i>Rangifer</i> populations can reach very high densities in the absence of predators.
Development of APDCE census technique (Hemming and Glenn 1968)	1967	First accurate census technique for caribou.
Publication of <i>Ecology of</i> <i>Caribou in Alaska</i> (Skoog 1968	1968 )	Review of historical literature of caribou in Alaska and <i>Rangifer</i> worldwide. Review and documentation of traditional knowledge. Case study of the Nelchina Caribou Herd from 1948–1962. Established the concept of "herds" as the basic unit of populations.

Table 1. Significant events that contributed to the evolution of caribou knowledge in Alaska.

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Event	Date	Contribution to development of knowledge and understanding of caribou
Publication of <i>The Caribou</i> (Kelsall 1968)	1968	Review of caribou in Northwest Territories of Canada including description of movements, population dynamics, and food habits.
Publication of detailed estimates of caribou numbers in Northwest Territories and recognition of "herds" in Canada (Thomas 1969)	1969	Recognition of 4 main "herds" in Northwest Territories of Canada.
Publication of The Population Dynamics of Newfoundland Caribou (Bergerud 1971)	1971	First detailed study of natality, mortality, and predation in caribou. Publication of technique for monitoring natality.
Crash of caribou herds in Alaska (c.f. Davis et al. 1979, Van Ballenberghe 1985)	1970 1975	Showed that caribou declines could be rapid, unexpected, and more difficult to explain than previously thought. Monitoring and research had been inadequate.
Wolf control to benefit moose in central Alaska (Gasaway et al. 1983)	1975 1982	Confirmed that caribou can increase rapidly when wolf numbers are reduced.
Implementation of statewide monitoring program in all major caribou herds using improved techniques (Davis et al. 1979, Davis 1980)	1977	Beginning of routine annual collections of data on recruitment and population size in Alaskan caribou herds.
Development and use of reliable long-range radio collars for caribou (Cameron et al. 1979, Davis and Valkenburg 1985)	1979	Over the next 10 years radio collars were deployed in all of Alaska's major herds and many minor herds as well. First opportunity for biologists to follow individual caribou.
Beginning of long-term research projects using radio collars (Davis and Valkenburg 1985, Adams et al. 1995)	1979	Results were slow in coming, but set the stage to answer questions about variability in mortality and natality rates, body condition, and predation in relation to weather and population density.
Increase of the George River Herd in Québec (Crête and Huot 1993)	1980s	This herd increased steadily to very high density on the summer range, and wolf numbers did not increase fast enough to control herd growth. Herd growth slowed due to poor summer nutrition.
Calf mortality studies in the Denali Herd (Adams et al. 1995)	1985	Grizzly bears and golden eagles are major predators of caribou calves in addition to wolves.

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Event	Date	Contribution to development of knowledge and understanding of caribou
Decline of caribou herds in Interior Alaska (Valkenburg et al. 1996, Mech et al. 1998)	1989 1993	Caribou declines were caused by increased predation as caribou calves became lighter in weight due to severe winter weather. Natality rate of caribou cows was reduced due to poor summer nutrition. Wolf numbers increased rapidly when prey species were more vulnerable.
Use of new piston helicopters for caribou capture and surveys	1992 5	New helicopters cut survey and capture costs by 50%.
Intense September snowstorm (Valkenburg et al. 1996)	1992	An unusually severe September snowstorm caused widespread and unusual caribou movement in Interior Alaska. In May 1993, natality rates were unusually low in many herds, and reached a new record low of 33% in the Delta Herd.
Decline of Northern Alaska Peninsula Herd (Sellers 1997)	1995 1998	The herd declined from high density. Body weights were low, condition was poor, and pneumonia was prevalent. There was no noticeable change in wolf numbers. A calf mortality study documented that neonatal losses to predators were relatively low initially but were then high for months.
Documentation of significant variation in size of Alaskan caribou calves (Valkenburg et al. 2000)	1995 -1998	Varying summer nutrition can account for virtually the entire range of variation in autumn weights of Alaskan caribou calves.
Application of molecular DNA techniques to caribou (Zittlau et al. 2000)	1998	There are at least 2 subspecies of caribou in Alaska, not one as previously thought. Interior Alaskan herds are similar genetically but Chisana Herd caribou are from woodland caribou stock.

1968, Urquhart 1989). The University of Alaska started its wildlife program in 1949 and the Cooperative Wildlife Research Unit opened in 1950 (D. R. Klein, Alaska Cooperative Wildlife Research Unit, personal communication). Various professional biologists visited Alaska and speculated about wildlife problems (c.f., Leopold and Darling 1953). With few data, biologists began to advance hypotheses explaining changes in caribou numbers and distribution, including predation by wolves (*Canis lupus*), icing conditions leading to die-offs, permanent emigration to other regions, overhunting, and destruction of winter range by wildfire (Leopold and Darling 1953, Skoog 1968, Harbo and Dean 1983). Agencies began to base management decisions on those concepts of caribou biology, and tried to increase caribou numbers by conducting organized predator control (Harbo and Dean 1983, Van Ballenberghe 1985, Valkenburg

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Fig 1. Names and locations of Alaskan caribou herds.

et al. 1994). The concept of caribou "herds" as "subpopulations" emerged, and fidelity to calving areas was recognized (Skoog 1968, Thomas 1969). Nonetheless, logistical considerations caused management and research activities in Alaska to be largely confined to the interior and south-central portions of the state and the statewide understanding of caribou distribution and dynamics remained poor. In 1957, the U.S. Fish and Wildlife Service began to document caribou distribution north of the Brooks Range (Olson 1958). This effort was greatly expanded in August 1958 with the disappearance of an aircraft piloted by the Regional Director of the U.S. Fish and Wildlife Service, Clarence Rhode (Olson 1959). Search flights were conducted intensively from 24 August to 31 November, and biologists and government agents recorded wildlife observations (Olson 1959:59). The missing aircraft was not found during the search, but a large amount of information on the largely unknown distribution of caribou in the Brooks Range and on the North Slope during autumn was acquired.

Although knowledge of caribou numbers and distribution in Alaska advanced considerably in the 1950s, the understanding of population dynamics and ecology remained poor. Caribou increased following wolf control, but documentation of predator numbers before and after control efforts was poor or lacking in many instances.

#### The 1960s

The 1960s produced some valuable insights into aspects of caribou ecology, but this decade was largely a period of stagnation in our understanding of caribou dynamics in Alaska. The state had taken over management jurisdiction for caribou and other nonmigratory game in 1960, and many experienced federal biologists left. Caribou numbers had increased greatly during the 1950s, and continued to be high in the early 1960s. There was less money for studies of wildlife, and management and research priorities largely shifted to moose (Alces alces). The long-term research on Fortymile and Nelchina caribou (Fig. 1) was terminated in the early 1960s, and few data were

collected subsequently (Skoog 1968, Van Ballenberghe 1985, Valkenburg et al. 1994). Research priorities also shifted from population dynamics to grazing ecology (Pegau and Hemming 1972; F. Dean, personal communication). Routine aerial and ground surveys to estimate caribou numbers and composition in interior and south-central Alaska were discontinued because of the lack of affordable aircraft, too few personnel, and changed priorities. Many biologists believed some caribou herds were too high and that local overuse of range would result in caribou moving to other areas (Skoog 1968). Other biologists, however, believed that the overpopulated herds would crash (Pegau and Hemming 1972). Because many managers thought that caribou moved in unpredictable ways, caribou were still considered to be largely "unmanageable." In addition, many biologists believed that predation did not play a major role in population regulation of caribou. At the time, most younger biologists were trained in areas with few large predators and they had little firsthand experience with predation.

Despite the lack of surveys and data collection in the 1960s, there were some major advances in our general knowledge about caribou, including publication of a landmark Ph.D. thesis (Skoog 1968), publication of the Project Chariot studies (Lent 1966), development of a caribou census technique (Hemming and Glenn 1968), and pioneering work on diseases and parasites in caribou and other species in Alaska (Neiland and Dukeminier 1972). During the late 1960s and early 1970s, results of a major effort by the Canadian Wildlife Service to investigate low numbers of caribou also were reported (Kelsall 1968, Parker 1972, Miller 1974, Dauphine 1976).

#### The 1970s

The 1970s can be characterized as a period of great turmoil that led to a renewed

emphasis on caribou research and a change in thinking about caribou ecology. By 1975, all of the major caribou herds in Alaska had declined. Because of the reduced emphasis on caribou in general, and on population dynamics in particular, however, basic data on caribou populations were lacking. Causes of caribou declines were largely unknown or at least unclear. In addition, as herds declined, many also were seriously overharvested (Davis et al. 1980, Van Ballenberghe 1985, Eberhardt and Pitcher 1992, Valkenburg et al. 1994). Those overharvests occurred because herd sizes were not adequately monitored and snowmobiles, which dramatically increased access, were becoming widely used for hunting caribou (Davis et al. 1980). A similar situation occurred in the Northwest Territories of Canada (Calef 1981:164).

The "caribou crisis" of the early to mid 1970s resulted in a renewed emphasis on research that was accompanied by a major advance in technology. Within a few years, massive amounts of new data accrued from reliable radio collars and improved survey and census techniques (Davis et al. 1979, Gasaway et al. 1983, Valkenburg et al. 1985). By the end of that decade, most of the 32 caribou populations (herds) in Alaska were mapped and their distribution and approximate sizes were determined (Davis 1980; Fig. 1). The important role of predation as a limiting factor also was becoming clearer (Gasaway et al. 1983). Because most herds in the state were recovering from low levels, and data from high-density herds in mainland North America were lacking, the role of nutrition as a limiting or regulating factor remained largely unknown. A debate raged between the so-called "predator people" and the "food fanciers," as biologists favoring 1 or the other of the 2 main regulatory factors in caribou populations were known (Bergerud 1978, Davis et al. 1983, Skogland 1985). At the end of the 1970s, many caribou biologists believed that in mainland North America, where the natural compliment of predators occurred, caribou populations were unlikely to be regulated or strongly limited by nutrition or food resources.

#### The 1980s

Although basic work defining caribou herds continued, and valuable confirmatory information accrued from expanded use of radio collars in studies of movement and predation, the 1980s yielded relatively few new insights on the factors that limit or regulate caribou numbers. Long-term monitoring of basic population parameters was, however, continuing in most of the economically important herds in the state, and a few herds (i.e., Delta, Denali, and Porcupine) were monitored intensively (Valkenburg et al. 1996, Whitten 1996, Mech et al. 1998). All of the major caribou herds in Alaska were increasing, and though population density was high in some herds, there was little evidence of nutrition becoming a limiting factor (Williams and Heard 1986, Davis and Valkenburg 1991). The Southern Alaska Peninsula Herd had declined apparently from nutrition-related causes. but the insular nature of its range, and relative lack of data made interpretation difficult (Post and Klein 1999). The predation versus food-limitation debate continued (White 1983, White and Luick 1984, Van Ballenberghe 1985, Messier et al. 1988, Bergerud and Ballard 1989). Some of the new information gained in the 1980s included evidence that, in addition to wolves, grizzly bears (Ursus arctos) and golden eagles (Aquila chrysaetos) were major predators of newborn and young caribou (Whitten et al. 1992, Adams et al. 1995).

#### The 1990s

Like the late 1970s, the early 1990s were a period of rapid accumulation of

knowledge about limiting and regulating factors in caribou populations. The boom in knowledge occurred for 2 main reasons. First, there was an abrupt and major change in the population trajectory of most of the interior Alaskan caribou herds and the George River Herd (Crête and Huot 1993, Valkenburg et al. 1996). Second, basic population parameters had been monitored in most Alaskan herds, and there were detailed data on changes in population size, natality, mortality, and cohort body weight from 2 herds (Adams et al. 1995, Valkenburg et al. 1996). Once it became clear that nutrition had played a major role in the decline of the interior herds, similar monitoring methods were applied to other herds in time to provide insights into declines in other areas (Valkenburg 1997). By the late 1990s, caribou in both the Northern Alaska Peninsula Herd and the Nelchina Herd were in chronically poor condition in autumn and the herds were declining from high densities.

Major lessons from the 1990s were: (1) small caribou herds can decline from any density because of changing weather patterns (Valkenburg et al. 1996, Lenart 1997, Mech et al. 1998); (2) some summers are better for caribou than others (Valkenburg et al. 1996, Lenart 1997, Valkenburg 1997); (3) when caribou density on summer range is high, body size and natality rate decline, although there can be time lags (Valkenburg 1997; Valkenburg et al. 2000); (4) wolf numbers can change rapidly as wolves take advantage of vulnerable prey (Boertje et al. 1996, Mech et al. 1998); (5) predation (especially by wolves) can result in the elimination or near elimination of caribou herds even where nutrition is good (Jenkins 1996; Gardner 1999; Adams, personal communication; Boudreau, personal communication); (6) in relatively small herds (i.e., < 5,000), predation is often a factor in population declines (Boertje et al. 1996, Valkenburg et

larger, adjacent herds, 1 herd probably has

al. 1996, Mech et al. 1998); (7) in larger herds (i.e.,  $\geq$  5,000) or where predation is light, caribou herds may decline from other factors such as disease (Sellers et al. 1998, Sellers 1999); and (8) virtually the entire range of body sizes of young Alaskan caribou can be explained by nutritional factors (Valkenburg et al. 2000). Many of these ideas were not new, but in the past were speculative, documented in other species, or there were no clear case histories to support them (c.f. Bergerud 1980). Much of what was discovered about the influence of nutritional factors on population dynamics and body size was previously documented for wild reindeer in Norway, albeit at higher densities in areas without large predators (c.f. Reimers 1997).

## The State of Caribou Knowledge at the Turn of the New Millennium

Over the last 25 years, several hypotheses about caribou and their population dynamics have been refuted. Natality is not fixed in caribou and wolf populations do not always expand to limit the growth of caribou herds before food shortages affect caribou numbers (c.f. Bergerud 1980, Crête and Huot 1993, Valkenburg et al. 1996, Adams and Dale 1998). The debate on predation versus food limitation is largely over. Either predation or food limitation, or a combination of both, can cause caribou herds to decline or stabilize. The single population hypothesis of Alaskan caribou (i.e., that all caribou in Alaska can be considered as a large, intermingling, population in the long term) has also not been supported (Skoog 1968). On the contrary, during the last 20 years of radiotelemetry, caribou "herds" clearly have been shown to be true populations or metapopulations (c.f. Valkenburg 1998). This is not to say that herds exist permanently. Within the last 20 years, 2 small herds in Alaska have virtually disappeared by being amalgamated with

been eliminated by predation, and 2 - 3 other small herds appear headed for elimination (Davis et al. 1991, Gardner 1997, Patten 1997; Boudreau, Alaska Department of Fish and Game, personal communication). In addition, no evidence exists to support the idea that caribou will permanently move away from areas of high density, and the movement of radiocollared caribou over the last 20 years has cast doubt on older interpretations of anecdotal records (Skoog 1968, Valkenburg 1997, Dau 1999). Drawing conclusions about the effect of human disturbances on caribou dynamics remains difficult. Although aircraft disturbance has largely been rejected as a significant influence (c.f. Klein 1973, Murphy et al. 1993), displacement of caribou from calving areas has occurred, and there could eventually be population consequences from such movements (c.f. Cameron et al. 1992). The hypothesis that caribou in Alaska are of one subspecies also appears to be incorrect (Banfield 1961; Zittlau, unpublished data).

Some older hypotheses about caribou dynamics have not been rejected. Predation by wolves has consistently been shown to be a critical factor limiting smaller herds of caribou (those numbering < 50,000). Although the idea was largely out of favor with most biologists during the 1960s and early 1970s, case studies in British Columbia, Yukon, and Alaska have shown that wolf predation can eliminate surplus caribou that would otherwise be available to hunters, and wolves (or brown bears and wolves together) can greatly reduce or even eliminate smaller herds (Gasaway et al. 1983, Farnell and MacDonald 1988, Seip 1992, Adams et al. 1995, Boertje et al. 1996, Boertje and Gardner 1998). The idea of caribou calving areas as focal points of herd distribution, and the general fidelity of females to calving areas also has been strongly supported during the last 25 years (Skoog 1968). Conversely, dispersal of female caribou from 1 herd to another is extremely rare (Valkenburg 1997, Boertje and Gardner 1998).

Some older ideas remain to be refuted or adequately tested. Many biologists and most managers traditionally have viewed population stability as desirable while others believed that caribou herds should be allowed to fluctuate naturally. At this point, there is no evidence to indicate that fluctuating caribou herds are "better" ecologically or more "natural" than stable ones. We now have some examples of relatively stable caribou herds (both large and small) that have not fluctuated much over several decades in addition to the many examples of herds that have fluctuated markedly (Whitten 1996, Valkenburg 1998). There are also a few examples of herds that have been extirpated by humans (Skoog 1968, Valkenburg 1998), and there are 2 herds in Alaska that appear to be headed for extirpation because of wolf predation (Gardner 1999; Boudreau, Alaska Department of Fish and Game, personal communication). Ecological differences between relatively stable herds, fluctuating herds, and herds that appear to be headed for extirpation are not well understood. Perhaps caribou are subject to population cycles, but this old hypothesis also remains untested.

There are also some new hypotheses that have emerged. Summer weather may have a major influence on nutrition, body condition, and reproduction in caribou, but many questions remain about the mechanisms involved (Russell et al. 1993, Valkenburg et al. 1996). There also is renewed interest in how climate changes and weather cycles may affect caribou populations (c.f. Gunn 1995).

#### DISCUSSION How We Have Learned

The development of knowledge about

caribou dynamics has not come gradually. Rather, there have been periods of stagnation with little or no progress, and shorter, more intense periods of confusion followed by significant growth in understanding. This pattern is probably the norm in most scientific endeavors. In some instances, application of new technology caused a great leap forward. Development of radio collars in the late 1970s is a prime example, but the widespread availability of helicopters in the early 1970s and the advent of less expensive helicopters in the early 1990s also have played a major role in expanding our knowledge of caribou dynamics. Development of personal computers in the 1980s revolutionized data storage, analysis, and communication. In some instances, application of relatively old technology applied in a methodical and comprehensive manner resulted in new insights. For example, the wide application of 1950s technology in photocensus techniques and systematic monitoring of body condition and population composition with methods largely developed in the 1940s and 1950s has made a large contribution to our understanding of caribou dynamics (Davis et al. 1979, Valkenburg et al. 2000). Experimentation (i.e., wolf control and caribou transplants to new ranges) also played a large role, as have unusual events (e.g., snowstorm and the short summer of 1992), which resulted in more intensive research on climatic effects (Boertje et al. 1996, Valkenburg et al. 1996). Clearly, advances in our understanding of caribou dynamics would not have come without the rapid population changes that took place in caribou herds.

Improved international communication among biologists also was important in advancing our knowledge of caribou dynamics. The lack of communication was apparent following the major declines of caribou in Alaska and Canada, and many biologists realized that research on caribou was hap-

hazard and in need of direction (Klein and White 1978). To improve communication, caribou and reindeer researchers also organized the North American Caribou Workshop that has been held every 2 - 3 years since 1983, and the previously organized International Reindeer/Caribou Symposium (now called the Arctic Ungulate Conference) was held more frequently. During the 1980s, there was also a realization in the wildlife profession that biologists had been rather lax in applying the scientific method in general, and hypothesis testing in particular, to wildlife research (Romesburg 1981, 1989; Gavin 1989; Hunter 1989; Matter and Mannan 1989). Those developments, and the discussion that surrounded them, caused biologists to better refine research questions, develop more rigorous approaches in study design, and instill more discipline in wildlife studies.

#### How Has Our New Knowledge Helped Management

Despite our improved knowledge and understanding of caribou dynamics, how well we can manage caribou numbers to benefit people is not clear. In a few instances, managers have tried to promote increases in caribou herds with some success, but results of management actions have not always been predictable (Valkenburg 1997). Caribou numbers can change because of the action of single factors, or combinations of multiple, interacting factors. Although there can be regional similarities in population processes due to weather, all caribou ranges are inherently different because of physiographic factors, variation in ungulate and predator abundance, varying quality and quantity of summer and winter range, differing movement patterns, and learned behaviors. So far, caribou managers have had the ability to influence only 2 factors (hunting and wolf predation). Currently, decisions on wolf management are primarily politically based and managers have little influence on such decisions. Where managers are able to successfully increase caribou herds, the public might reasonably expect that hunting also can prevent herds from overusing their ranges and declining. Nonetheless, regulation of the upper bound of caribou herd size through hunting is difficult because of problems with hunter access and caribou distribution. The road system in Alaska generally does not provide effective access to caribou herds, and where it does, caribou movements may prevent hunters from reducing caribou numbers in time to prevent higher than desired populations. This situation is prevalent throughout most caribou ranges in North America. For the foreseeable future, the primary role of wildlife biologists will continue to be providing for caribou hunting while ensuring that hunting does not cause herds to decline to lower than desired levels. In a few instances, biologists may be able to manage caribou herds for increased harvest, but our most important secondary role will be providing information to people about why a particular caribou herd may be decreasing, and explaining the rationale for hunting regulations. To fulfill our primary role, little specific information is needed. An annual estimate of recruitment and sex composition, a periodic census, and harvest monitoring will suffice. Much more information is needed to justify predator control, or if we are expected to explain why a herd may be decreasing, especially if harvest needs to be restricted. Naturally increasing herds usually require no explanation.

#### Lessons for the Future

There are valuable lessons we should have learned from the last 50 years of caribou management and research in Alaska. First and foremost is that without basic monitoring of population parameters,

studying limiting factors is difficult. Although investigating weather, climate, other physical factors, and sometimes body size, after the fact is possible, resurrecting figures on recruitment, population size, natality, and mortality is not. We now have 20 years of continuous population data (census and autumn composition counts) in most of the economically important caribou herds in Alaska, and we need to continue to ensure those data are collected. Second, we need to continue long-term monitoring of body condition in as many of the same herds as possible. We spent many years arguing over predation versus nutrition when simple condition data could have settled many questions. We also need to realize that rare events can provide much information and we need to take advantage of these events when they occur. Although it may mean changing schedules and reprogramming funds, the return can be immense.

The primary responsibility for monitoring population parameters and body condition will always fall to government agencies because wildlife management is a matter of public trust. In Alaska, long-term population monitoring will continue to be the responsibility of the State and must continue to be a priority. Long-term research is also most likely to be conducted by the State. Federal agencies, with their generous budgets, are a valuable aid when short-term money is needed to take advantage of rare events and rapid changes in wildlife populations, but longer-term funding is often a problem. University research, particularly by graduate students, has been the most efficient way to gather information on discreet topics, especially where work is labor intensive, new technologies must be tested, or where an interdisciplinary approach is required. During the last 20 years, many of the advances in our knowledge of caribou have come from the successful cooperation of the Alaska Department of Fish and Game, federal agencies, and universities.

Finally, there have been some critically important lessons about our dealings with each other in our search for the truth about caribou dynamics. The first is that it is all right to be wrong. Even some of the most carefully done research generates plausible hypotheses that later turn out to be wrong. This is part of the process, and should not be cause for embarrassment or defensiveness. Conversely, formulating ideas based on inadequate review of research already completed, or clinging to old ideas despite clear evidence to the contrary is wrong. Thoroughly reviewing the literature is not difficult, and failure to do so results in wasted time, energy, and money. We owe it to those who have come before us to at least be familiar with their work and ideas. Next, it is wise not to condemn those with seemingly far-fetched ideas, partly because they may be right, but also because such condemnation stifles creativity, especially in younger people. Finally, we need to realize that everyone has something different to offer. Some of us are methodical plodders, and some of us are compulsive leapers and bounders, and there really is not that much we can do about it.

#### ACKNOWLEDGEMENTS

I thank D. Klein, F. Dean, J. Davis, R. Farnell, and R. Boertje for ideas and/or historical information. D. Klein and J. Davis, although different in almost every way, have both played a large roll in my education, and in the evolution of knowledge about caribou in Alaska.

#### REFERENCES

ADAMS, L. G., and B. W. DALE. 1998. Reproductive performance of female Alaskan caribou. Journal of Wildlife Management 62:1184–1195.

\_\_\_\_, F. J. SINGER, and B. W. DALE.

1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584–594.

BANFIELD, A. W. F. 1954. Preliminary investigation of the barren-ground caribou. Canadian Wildlife Service, Wildlife Management Bulletin, Series 1, 10A and 10B. Ottawa, Ontario, Canada.

- \_\_\_\_\_. 1961. A revision of the reindeer and caribou, genus *Rangifer*. National Museum of Canada Bulletin 177, Biology Series 66. Ottawa, Ontario, Canada.
- BERGERUD, A. T. 1971. The population dynamics of Newfoundland caribou. Wildlife Monographs 25.
  - J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

  - , and W. B. BALLARD. 1989. Wolf predation on the Nelchina caribou herd. Journal of Wildlife Management 53:251– 259.
- BOERTJE, R. D., and C. L. GARDNER. 1998.
  Factors limiting the Fortymile Caribou Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-24-1 through W-24-5. Study 3.38. Juneau, Alaska, USA.
  - P. VALKENBURG, and M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474– 489.
- BURCH, E. S. 1999. The Inupiaq Eskimo nations of northwest Alaska. Univer-

sity of Alaska Press, Fairbanks, Alaska, USA.

- CALEF, G. W. 1981. Caribou and the barren lands. Canadian Arctic Resources Committee/Firefly Books. Ottawa, Ontario, Canada.
- CAMERON, R. D., D. J. REED, J. R. DAU, and W. T. SMITH. 1992. Redistribution of calving caribou in response to oilfield development. Arctic 45:338-342.
- , K. R. WHITTEN, W. T. SMITH, and D. D. ROBY. 1979. Caribou distribution and group composition associated with the Trans-Alaska Pipeline. Canadian Field-Naturalist 93:155–162.
- CLARKE, C. H. D. 1940. Biological investigation of the Thelon Game Sanctuary. National Museum of Canada Bulletin 96, Biology Series 25. Ottawa, Ontario, Canada.
- CRÊTE, M., and J. HUOT. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71:2291-2296.
- DAU, J. R. 1999. Western Arctic Herd caribou management report of surveyinventory activities. Pages 160–185 in M. V. Hicks, editor. Alaska Department of Fish and Game. Federal Aid in Wildlife. Restoration. Grants W-24-5 and W-27-1. Study 3.0. Juneau, Alaska, USA.
- DAUPHINE, C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. Canadian Wildlife Service Report, Series 38. Ottawa, Ontario, Canada.
- DAVIS, J. L. 1980. Status of Rangifer in the USA. Pages 793-797 in E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, Roros, Norway. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway.

- , and P. VALKENBURG. 1985. Qualitative and quantitative aspects of natural mortality of the Western Arctic Caribou Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-17-11 through W-22-3. Juneau, Alaska, USA.
- \_\_\_\_\_, and \_\_\_\_\_. 1991. A review of caribou population dynamics in Alaska emphasizing limiting factors, theory, and management implications. Pages 184– 209 in C. E. Butler and S. P. Mahoney, editors. Proceedings of the Fourth North American Caribou Workshop, 1989. Newfoundland and Labrador Wildlife Division, St. John's, Newfoundland, Canada.
- \_\_\_\_\_, \_\_\_\_, and R. D. BOERTJE. 1983. Demography and limiting factors of Alaska's Delta caribou herd. Acta Zoologica Fennica 175:135–137.
- , \_\_\_\_\_, and S. J. HARBO. 1979. Refinement of the aerial photo-direct count-extrapolation caribou census technique. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grant W-17-11. Juneau, Alaska, USA.
- , \_\_\_\_, M. E. MCNAY, R. M. BEASLEY, and V. L. TUTTERROW. 1991. Demography of the Delta Caribou Herd under varying rates of natural mortality and human harvest and assessment of field techniques for acquiring demographic data. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-22-5 through W-23-3. Juneau, Alaska, USA.
- , \_\_\_\_, and H. V. REYNOLDS. 1980. Population dynamics of Alaska's Western Arctic Caribou Herd. Pages 595-604 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/

Caribou Symposium, Roros, Norway. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway.

- EBERHARDT, L. L., and K. W. PITCHER. 1992. A further analysis of Nelchina caribou and wolf data. Wildlife Society Bulletin 20:385-395.
- FARNELL, R., and J. MACDONALD. 1988. The influence of wolf predation on caribou mortality in Yukon's Finlayson Caribou Herd. Proceedings of the Third North American Caribou Workshop. Alaska Department of Fish and Game. Wildlife Technical Bulletin 8:52–70. Juneau, Alaska, USA.
- GARDNER, C. L. 1997. Fortymile Herd caribou management report of surveyinventory activities. Pages 126–147 in M. V. Hicks, editor. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-3 and W-24-4. Juneau, Alaska, USA.
- GASAWAY, W. C., R. O. STEPHENSON, J. L. DAVIS, and O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in Interior Alaska. Wildlife Monographs 84.
  - GAVIN, T. A. 1989. What's wrong with the questions we ask in wildlife research. Wildlife Society Bulletin 17:345-350.
  - GUNN, A. 1995. Responses of Arctic ungulates to climate change. Pages 89–104 in D. L. Peterson and D. R. Johnson, editors. Human ecology and climate change: people and resources in the far north. Taylor and Francis, Washington, D.C., USA.
  - HARBO, S. J., and F. C. DEAN. 1983. Historical and current perspectives on wolf

management in Alaska. Pages 51-65 in L. N. Carbyn, editor. Wolves in Canada and Alaska: their status, biology, and management. Canadian Wildlife Service Report, Series 45. Ottawa, Ontario, Canada.

- HEMMING, J. E., and L. P. GLENN. 1968. Caribou Report. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-15-2 and W-15-3. Juneau, Alaska, USA.
- HUNTER, M. L. 1989. Aardvarks and arcadia: two principles of wildlife research. Wildlife Society Bulletin 17:350-351.
- JENKINS, K. J. 1996. Population dynamics of the Mentasta Caribou Herd, Wrangell-St. Elias National Park and Preserve: Progress Report and Preliminary Assessment. WRST Research and Management. Report 95-1. U.S. National Park Service, Anchorage, Alaska, USA.
- KELSALL, F. 1968. The migratory barrenground caribou of Canada. Canadian Wildlife Service Monograph 3. Ottawa, Ontario, Canada.
- KLEIN, D. R. 1968. The introduction, increase, and crash of reindeer on St. Mathew Island. Journal of Wildlife Management 32:350-367.
  - . 1973. The reaction of some northern mammals to aircraft disturbance. Pages 377–383 *in* Eleventh International Congress of Game Biologists, Stockholm, Sweden.
  - , and R. G. WHITE, editors. 1978. Parameters of caribou population ecology in Alaska: Proceedings of a Symposium and Workshop. Biological Papers of the University of Alaska, Fairbanks, Alaska, USA.
- LENART, B. 1997. Effects of weather on forage productivity and nutrition within the range of the Chisana Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Re-

port. Grants W-24-3 through W-24-5. Study 3.41. Juneau, Alaska, USA.

- LENT, P. C. 1966. The caribou of northwestern Alaska. Pages 481–517 in N. J. Willimovsky and J. N. Wolfe, editors. Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Commission, Washington, D.C., USA.
- LEOPOLD, A. S., and F. F. DARLING. 1953. Wildlife in Alaska. Ronald Press, New York, New York, USA.
- MATTER, W. J., and R. W. MANNAN. 1989. More on gaining reliable knowledge: a comment. Journal of Wildlife Management 53:1172–1176.
- MECH, L. D., L. G. ADAMS, T. J. MEIER, J. W. BURCH, and B. W. DALE. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota, USA.
- MESSIER, F., J. HUOT, D. LEHENAFF, and S. LUTTICH. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. Arctic 41:279-287.
- MILLER, F. L. 1974. Biology of the Kaminuriak population of barren-ground caribou. Part 2. Canadian Wildlife Service Report, Series 31. Ottawa, Ontario, Canada.
- MURIE, O. J. 1935. Alaska-Yukon caribou. U.S. Department of Agriculture, Bureau of Biological Surveys, North American Fauna 54. U.S. Government Printing Office, Washington, D.C., USA.
- MURPHY, S., R. G. WHITE, B. A. KUGLER, J. A. KITCHENS, M. D. SMITH, and D. S. BARBER. 1993. Pages 479–486 in Behavioral effects of jet aircraft on caribou in Alaska. Proceedings of the Sixth International Congress on Noise as a Public Health Problem, Arcueil Cedex, France.
- NEILAND, K. A., and C. DUKEMINIER. 1972. A bibliography of the parasites, dis-

eases and disorders of several important wild ruminants of the northern hemisphere. Alaska Department of Fish and Game, Wildlife Technical Bulletin 3. Juneau, Alaska, USA.

- OLSON, S. T. 1958. Caribou management studies—movements, distribution and numbers. U.S. Fish and Wildlife Service, Federal Aid in Wildlife Restoration. Job (job 2c) Completion Report, Project W-3-R-12, Volume 12(3). Juneau, Alaska, USA.
- . 1959. Caribou management studies—movements, distribution and numbers.
   U.S. Fish and Wildlife Service, Federal Aid in Wildlife Restoration. Job (job 1a) Completion Report. Project W-3-R, Volume 13(3). Juneau, Alaska, USA.
- PARKER, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part 1. Canadian Wildlife Service Report, Series 20. Ottawa, Ontario, Canada.
- PATTEN, S. 1997. Caribou management report-Kilbuck Herd. Report of surveyinventory activities. Pages 98–107 in M. V. Hicks, editor. Alaska Department Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-3 and W-24-4. Juneau, Alaska, USA.
- PEGAU, R. E., and J. E. HEMMING. 1972. Caribou investigations—analysis of range. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-17-2 and W-17-3. Juneau, Alaska, USA.
- POST, E., and D. R. KLEIN. 1999. Caribou calf production and seasonal range quality during a caribou population decline. Journal of Wildlife Management 63:335– 345.
- RAUSCH, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. American Zoologist 7:253–265.

REIMERS, E. 1997. Rangifer population

ecology: a Scandinavian perspective. Rangifer 17:105–118.

- ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293-313.
- RUSSELL, D. R., A. M. MARTELL, and W. A. C. NIXON. 1993. Range ecology of the Porcupine Caribou Herd in Canada. Rangifer Special Issue 8.
- SCOTT, R. F., E. F. CHATELAIN, and W. A. ELKINS. 1950. The status of Dall sheep and caribou in Alaska. Transactions of the North American Wildlife Conference 15:612-626.
- SEIP, D. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70:1494–1503.
- SELLERS, R. A. 1997. Northern Alaska Peninsula Herd caribou management report of survey-inventory activities. Pages 37-48 in M. V. Hicks, editor. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-3 and W-24-4. Study 3.0. Juneau, Alaska, USA.
- . 1999. Northern Alaska Peninsula caribou management report of survey-inventory activities. Pages 35-46 in M.
   V. Hicks, editor. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Grants W-24-5 and W-27-1. Study 3.0. Juneau, Alaska, USA.
- P. VALKENBURG, R. L. ZARNKE, and R. C. SQUIBB. 1998. Natality and early calf mortality of Northern Alaska Peninsula caribou, 1998. Final Report. Cooperative Agreement 98-079. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- SINIFF, D. B., and R. O. SKOOG. 1964.

Aerial censusing of caribou using stratified random sampling. Journal of Wildlife Management 28:391–401.

- SKOGLAND, T. 1985. The effects of densitydependent resource limitation on the demography of wild reindeer. Journal of Animal Ecology 54:359–374.
- SKOOG, R. O. 1956. Range, movements, population, and food habits of the Steese-Fortymile caribou herd. M.S. Thesis, University of Alaska, Fairbanks, Alaska, USA.
- \_\_\_\_\_. 1968. Ecology of the caribou in Alaska. Ph.D. Thesis, University of California, Berkeley, California, USA.
- THOMAS, D. C. 1969. Population estimates and distribution of barren-ground caribou in Mackenzie District, NWT, Saskatchewan, and Alberta—March to May, 1967. Canadian Wildlife Service Report, Series 9. Ottawa, Ontario, Canada.
- URQUHART, D. 1989. History of research. Pages 95–102 in E. Hall, editor. People and caribou in the Northwest Territories. Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- VALKENBURG, P. 1997. Investigation of regulating and limiting factors in the Delta Caribou Herd. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-23-5 and W-24-1 through W-24-4. Study 3.37. Juneau, Alaska, USA.
  - . 1998. Herd size, distribution, harvest, management issues, and research priorities relevant to caribou herds in Alaska. Rangifer Special Issue 10:125-129.
  - D. A. ANDERSON, J. L. DAVIS, and D. J. REED. 1985. Evaluation of an aerial photocensus technique for caribou based on radiotelemety. Pages 287-299 in T. C. Meredith and A. M.

Martell, editors. McGill Subarctic Research Paper 40. McGill University, Montreal, Québec, Canada.

- \_\_\_\_\_, J. L. DAVIS, and D. G. KELLEYHOUSE. 1994. Case history of the Fortymile Caribou Herd. Rangifer 14:11-22.
- , —, J. M. VER HOEF, R. D.
   BOERTJE, M. E. MCNAY, R. M. EAGAN, D.
   J. REED, C. L. GARDNER, and R. W.
   TOBEY. 1996. Population decline in the Delta caribou herd with reference to other Alaskan herds. Rangifer Special Issue 9:53-62.
- , T. H. SPRAKER, M. T. HINKES, L. H. VAN DAELE, R. W. TOBEY, and R. A. SELLERS. 2000. Increases in body weight and nutritional status of transplanted Alaskan caribou. Rangifer Special Issue 12:133-138.
- VAN BALLENBERGHE, V. 1985. Wolf predation on caribou—the Nelchina case history. Journal of Wildlife Management 49:711-720.
- WHITE, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377– 384.
- , and J. R. LUICK. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. Symposia of the Zoological Society of London 51:215-232.
- WHITTEN, K. R. 1996. Ecology of the Porcupine Caribou Herd. Rangifer Special Issue 9:45–52.
- ....., G. W. GARNER, F. J. MAUER, and R. B. HARRIS. 1992. Productivity and early calf survival in the Porcupine Caribou Herd. Journal of Wildlife Management 56:201–212.
- WILLIAMS, T. M., and D. C. HEARD. 1986. World status of wild *Rangifer tarandus* populations. Rangifer Special Issue 1:19-28.
- ZITTLAU, K., J. COFFIN, R. FARNELL, G. W.

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KUZYK, and C. STROBECK. 2000. Determination of the genetic relationships of caribou populations by DNA typing using micro-satellites. Rangifer Special Issue 12:59-62.