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A REVIEW OF CARIBOU POPULATION DYNAMICS IN ALASKA EMPHASIZING LIMITING FACTORS, THEORY, AND MANAGEMENT IMPLICATIONS

James L. Davis, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701 U.S.A.

Patrick Valkenburg, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701 USA

<u>Abstract</u>: Alaska's 29 recognized caribou (<u>Rangifer tarandus granti</u>) herds are classified to identify those that are both migratory and inhabit areas where moose (<u>Alces alces</u>) (or other ungulates) are important alternate prey. During the time that detailed demographic data have been obtained (i.e., 1960s-1980s), natural mortality and human-induced mortality have varied more and have more influenced Alaska's caribou herd demographics than have natality changes. Dispersal has not significantly influenced population dynamics during this time and has not been consistent with theory in the caribou literature. Detailed demographic data have been obtained primarily during low and increasing phases of populations. Recent conclusions regarding limiting and regulating factors are compared and contrasted with past reviews of Alaskan caribou population dynamics.

INTRODUCTION

For discussion at the 4th North American Caribou Workshop, caribou in North America were envisioned as comprising 3 ecotypes (F. Messier, pers. commun.): ecotype 1 - woodland caribou (<u>R.t caribou</u>) living in association with alternate ungulate prey (e.g., British Columbia caribou); ecotype 2 - migratory caribou herds that inhabit areas also used by alternate ungulate prey (particularly moose) (e.g., Alaska caribou); and ecotype 3 - migratory caribou herds having limited contact with alternate ungulate prey (e.g., the George River Herd in Quebec/Labrador).

This paper discusses population dynamics in the Alaskan caribou ecotype. The theory and empirical data for Alaska caribou population dynamics through the 1970's have been previously and intensively reviewed (e.g., Skoog 1968, Bergerud 1980, and others). Hence, we will only summarize recent changes in population size and trend for Alaska caribou herds. In discussing limiting versus regulating factors, we will summarily review the 3 components of population dynamics, natality, mortality, and dispersal, as they relate to the population dynamics of Alaska caribou. In addition we will (1) discuss some existing theories of caribou population dynamics, (2) discuss how recent empirical findings relate to these theories, (3) evaluate the most tenable extension of the theories into management practices, and (4) attempt to identify factors currently limiting our understanding of caribou population dynamics.

DEFINITIONS

For standardization at this workshop, we use definitions proposed by F. Messier (pers. commun.) for limiting factors, regulating factors, and population control. In addition, we define population dynamics.

<u>Population dynamics</u> - The process by which births, deaths, and dispersal change population size over time.

Limiting factors - Any processes that quantifiably affect (restrict) population growth. They induce year-to-year changes in the rate of population growth and, by extension, in animal abundance. They may be stochastic or with reproducible density relationships.

<u>Regulating factors</u> - Any density-dependent processes that ultimately keep populations within normal density ranges. Thus, regulating factors are a subset of limiting factors characterized by negative-feedback mechanisms, that depress population growth as animal abundance increases.

<u>Population control</u> - Connotes a planned attempt by humans to manipulate population size through hunting or culling.

POPULATION DYNAMICS AND LIMITING FACTORS

During the early and mid-1970s most Alaskan herds declined (Fig. 1, Table 1, 2, 3). The statewide population declined from 415,000 in 1970 to 255,000 in 1977 (a decline of 39%, r = -0.08). In contrast most herds increased from 1977 to 1989. The statewide population grew from 255,000 in 1977 to 729,000 in 1989 (200%, r = 0.09). The historical records and prehistorical evidence suggest that frequent and dramatic population changes have always occurred in Alaskan caribou herds.



Fig. 1. Distribution of caribou herds in Alaska and major prey species in herd ranges (C = caribou, M = moose, S = sheep).

The most important factors that explain changes in caribou abundance in Alaskan herds from t (year 1) to t + 1 (year 2) have varied over time and among herds within any given time. Reasons for the declines during the 1970s have been reported, discussed, and debated repeatedly (e.g., Bergerud 1978, Doerr 1980, Gasaway et al. 1983). There is general consensus that exploitation by humans and predation

	Population siz			
Herd	1970	1977	1989	
			<u></u>	
Adak Alaska Peninsula (N)	110	250 10,400	500 20,000	
Alaska Peninsula (S) Alaska Peninsula (Total) Andreafsky	14,000	7,600 18,000; 3,000	5,500 26,000 250	
Beaver Mountains Big River	2,000	2,000	2,000	
Central Arctic Chisana	1,500	5,000 1,500	16,000 1,700	
	5,000	2,500	10,200	
Denali Fortymile Kenai Lowlands	4,500 10,000	1,000 6,000 80	3,000 22,500 100	
Kenai Mountains Kilbuck Mountains	300	300 1,000	400 950	
Kokrines Hills Kuskokwim Mountains Macomb Plateau Mentasta Mulchatna	2,500 8,000	900 2,500 10,000	800 300 800 2,000 66,000	
Nelchina Porcupine Rainy Pass Ray Mountains Sunshine Mountains	25,000 100,000	14,000 100,000 3,000 200 750	40,000 175,000 2,500 700 500	
Teshekpuk Tonzona		8,000	11,000 1,000	
Western Arctic White Mountains Yanert	242,000	75,000	343,000 1,000 600	
Total	414,910	255,580	729,050	

Table 1. Recognized caribou herds in Alaska and population size in 1970, 1977, and 1989.

Herd	1970-77 r	1977-89 r
Adak	0.12	0.06
Alaska Peninsula (Total)	0.04	0.03
Alaska Peninsula (N)		0.05
Alaska Peninsula (S)		-0.01
Andreafsky ^a		-0.21
Central Arctic		0.10
Delta	-0.10	0.12
Denali	-0.21	0.09
Fortymile	-0.13	0.14
Kenai (lowlands)		0.03
Kenai (mountains)	0.00	0.02
Kilbuck Mountains ^a		-0.03
Macomb Plateau		-0.01
Mentasta	0.00	0.00
Mulchatna	0.03	0.16
Nelchina	-0.08	0.09
Porcupine	0.00	0.05
Rainy Pass		-0.02
Ray Mountains		0.10
Teshekpuk		0.26
Western Arctic	-0.17	0.13
Total population	-0.08	0.09
Mean of all herds	-0.05+0.10(SD)	0.06+0.09(SD)

Table 2. A comparison of exponential herd growth for Alaskan caribou herds from 1970 to 1977 and 1977 to 1989.

^a Census data are probably not reliable.

increased mortality rates and lowered recruitment rates commonly during the declines of the 1970's. There is less consensus over the role of weather and nutritional limitation. Debate continues over the role of predation as a proximate versus ultimate limiting factor. Also, serious debate continues over the role of density-dependent factors in the declines and increases. However, little compelling evidence for density dependent <u>regulation</u> has occured for the range of population densities that have been monitored. Albeit, evidence of density-dependent <u>responses</u> in Alaskan caribou have been reported (see Valkenburg et al., Davis et al., this workshop).

During the post-1977 population increase in Alaskan caribou, preclusion of excessive exploitation of caribou by humans has undoubtedly contributed to the rate of caribou population growth. Also, in general wolf populations were low or at moderate levels and weather has been favorable during the increases of the 1980s. Birth rate has varied less than natural mortality rate through both the decline and growth phases of the Alaskan population. Apparently dispersal played no measurable role in the recent population declines or increases.

REGULATING FACTORS

To date it appears that limiting factors have more influence on population dynamics of Alaska caribou than have regulating factors. Assuredly, caribou in Alaska show signs of resource limitation (i.e., negative feedback to nutritional limitation) that correlate with population size (density). However, these responses have not been demonstrated to create measurable population regulation. From available evidence for Alaska caribou, we conclude that neither natality, mortality, nor dispersal operate in a very sensitive, linear, or curvilinear manner throughout the population density range we have monitored.

Herd No.	Herd name	Herd size	Population trend	Harvest in 1987-88	Range km²	Density caribou/km ²
1	Adak	464-497	Stable	121	750	0.6
2	Alaska Peninsula (N)	20.000	Stable	2,300	23,000	0.9
3	Alaska Peninsula (S)	5,500	Declining	300	5,000	1.1
4	Andreafsky	250	Unknown	Unknown	-•	
5	Beaver Mountains	2,000	Unknown	17		
6	Big River	750	Unknown	43		
ິ 7	Central Arctic	16,000	Increasing	575	40,000	0.4
8	Chisana	1,700	Stable	82	4,000	0.4
9	Delta	10,200	Stable	667	11,000	0.9
10	Denali	3,000	Increasing	0	8,000	0.4
11	Fortymile	22,500	Increasing	260	50,000	0.5
12	Kenai Lowlands	100	Stable	4		
13	Kenai Mountains	400	Increasing	50		
14	Kilbuck Mountains	950	Increasing	75		
15	Kokrines Hills	800	Unknown	5		
16	Kuskokwim Mountains	300	Unknown	Unknown		
17	Macomb Plateau	800	Stable	57	1,500	0.5
18	Mentasta	2,000	Declining	112	4,000	0.5
19	Mulchatna	66,000	Increasing	2,000	78,000	0.9
20	Nelchina	40,317	Increasing	1,747	40,000	1.0
21	Porcupine	175,000	Increasing	3,500	259,000	0.7
22	Rainy Pass	2,500	Unknown	85		
23	Ray Mountains	700	Unknown	5	6,500	0.1
24	Sunshine Mountains	500	Unknown	2		
25	Teshekpuk	11,000	Unknown	750	16,500	0.7
26	Tonzona	1,000	Unknown	45		
27	Western Arctic	343,000	Increasing	10,000	360,000	1.0
28	White Mountains	1,000	Increasing	10	5,000	0.2
29	Yanert	600	Stable	113	1,950	0.3

Table 3. Population size, range size, and density of Alaska caribou herds, 1989.

Graphic depiction is the most concise way for us to present our view

of the generalized relationship of density to natality, mortality, and dispersal for Alaska caribou. We contrast the classic textbook-like relationship of natality (Fig. 2), for white-tailed deer (McCullough 1979), which is linear and inversely densitydependent with that we envision for Alaska caribou. We did not graphically depict what we envision as the density/mortality relationship for caribou. We envision the general curve for that relationship as approaching a reflection of the natality/density curve in Fig. 2. Mortality appears to be low and relatively constant at low and medium density with a sharp inflection occurring at some point in the high-density range.



Fig. 2. Comparison of the natality/density relationship for white-tailed deer (after McCullough 1979) with that envisioned for caribou.

Regarding dispersal, we use Bergerud's (1980) envisioned model (which is similar to that of Skoog (1968) and Haber and Walters (1980)) to depict a consensus model for dispersal based on the literature (Fig. 3). There is little empirical data available for evaluation of the dispersal model. Since the 1960s, only Alaska's Southern Alaska Peninsula Herd (SAPH) has reached or exceeded the model's dispersal threshold density. The SAPH apparently exceeded a density of 2 km^2 , did not disperse, and declined by 250%, apparently from resource limitation (Pitcher and Johnson 1989; Johnson, in press). We have never verified density-dependent dispersion in Alaska caribou the in context of mass emigration/immigration (albeit anecdotal literature abounds with references, e.g., Skoog 1968). Davis et al. (1978) reviewed the circumstantial evidence for the assumed mass emigration from the Fortymile Herd in 1957 and 1964 (Skoog 1968) and concluded that there was no evidence to conclude that any net emigration had occurred. Similarly, the presence of radio-collared individuals has helped demonstrate that no measurable net emigration/immigration has occurred when several herds (e.g., Delta, Porcupine, Nelchina, Mentasta) have made major incursions into adjacent herd ranges and overlapped in seasonal distribution (primarily in winter). Similar incursions had been considered evidence for net emigration in the past.

Because population regulation is central to much general population dynamics theory, it seems logical to hypothesize that regulating factors must operate in caribou population dynamics. Caribou managers in Alaska have gone much further than that in the past. During the 1960s and early 1970s, management philosophy and policy in Alaska incorporated much general population regulation theory that proved to be inappropriate for caribou. This, among other factors, led to overharvest of caribou and decline of the statewide population.



Fig. 3. The population growth limits of caribou envisioned as a staircase of limits imposed by predation and dispersion and crash-decline caused by density-dependent food shortage (from Bergerud 1980). Bergerud (1978) opined that 3 points contributed to the Alaskan caribou decline: (1) the belief that large herds would not be overharvested, (2) underestimating the extent of calf mortality when predators were abundant, and (3) the belief that food supplies set carrying capacity for caribou populations which, consequently, had to be hunted heavily to prevent the animals from overgrazing habitat and declining in number. These 3 points certainly contributed to the decline, and intertwined in all 3 points was the belief of density-dependent compensatory mortality and inversity (in terms of productivity and survival).

ALASKA CARIBOU AS AN ECOTYPE

To consider all caribou herds in Alaska as 1 ecotype assumes that all herds are more similar to one another than to herds identified as separate ecotypes. We subjectively categorized caribou herds in Alaska as being part of predator-prey systems where the major prey was either 1) caribou, 2) moose and caribou, or 3) sheep (<u>Ovis</u> <u>dalli</u>), moose, and caribou (Fig. 1). Herds characteristic of the moose-caribou system, i.e., the "Alaskan ecotype" number 16 of 29 total (Fig. 1). Hence, 55% of Alaska's herds fit the Alaska ecotype definition, but these herds contain only 15% of the statewide population.

Inferring the existence of different ecotypes of caribou implies to us that the systems to which the ecotypes are a part have been evolutionarily divergent from one another. Also implied is that the ecotypes have existed as they are for sufficient time for system "norms" to have evolved. We believe these implied assumptions about 1 caribou ecotype for Alaska may be largely invalid. The "tundra herds" in Alaska (i.e., those whose distributions reach the coastline) prior to the 1900s apparently never had significant moose as alternate prey in the past several thousand years. Most predator/prey systems associated with Alaska caribou herds today have existed no longer than a century, many only since the 1930s. Much of the present moose distribution has existed for only 50-100 years.

Biologists studying moose systems in interior Alaska (e.g., Van Ballenberghe 1987; Gasaway, pers. commun.) have inferred that historically much of interior Alaska was characterized by a low moose-low wolf (including grizzly (<u>Ursus arctos</u>) and/or black (<u>Ursus</u> <u>americanus</u>) bears) equilibrium with caribou appearing as secondary alternate prey. From circumstantial evidence we have inferred an opposing model which considers caribou as the predominant prey during the prehistory past in most of Alaska. This model was derived from a review of the archaeologic evidence for the relative importance of moose and caribou to Natives in Alaska during late prehistoric times and assumes that the relationships between wolves (<u>Canis lupus</u>) and bears to ungulate prey paralleled that of man.

Yesner (1989) recently reviewed the archaeological evidence from interior and southcentral Alaska (largely the Pleistocene refugium in east-central Alaska and adjacent Yukon). Overwhelmingly his archaeological evidence showed that caribou and not moose were the predominant prey of native people in Interior Alaska throughout late prehistory and early historical times. Yesner (1989) succinctly outlined the background of native peoples dependence on moose in late pre-history times, and he concluded that reconsideration was warranted. By inserting (predators) each time Athapaskan appears, in Yesner's (1989) summary, one can conjecture the character of the large mammal predator/prey systems in the past:

"Many descriptions of lifestyles (including those of predators) in the western subarctic region have been built on the premise that the hunting and use of the moose was a central feature of those lifestyles. While this may be true, it is worthwhile to question the time depth that underlies this adaptation and the degree to which it may have applied to former societies (predator populations) inhabiting the boreal forest region. Any such effort must include an analyses of available faunal from archeological sites in that region. remains Α consideration of the faunal record suggests that the intensive utilization of moose is relatively new in the western boreal forest, or at least was not widely characteristic of the late Holocene period. Thus it cannot be assumed that the archeologically designated late prehistoric "Athapaskan tradition" (low wolf/moose equilibrium) was isomorphic with modern subsistence regimes (predator/prey systems).

"To the degree to which large game played a central role in Athapaskan lifestyles (predator population systems), it was caribou, rather than moose, that seems to have dominated the northern ecotonal region... Historical factors, primarily involving widespread fires, habitat disturbance and impacts on predators, seem to be most responsible for the increase in moose numbers during the past century."

The relevance of Yesner's (1989) findings to this paper is two-fold. First, much of the literature on Alaska caribou population dynamics may be more characteristic of caribou ecotypes 1 or 3 than the Alaska ecotype (ecotype 2). Secondly, even for the Alaska ecotype, the ecotype may be very young (no more than 50 to several hundred years old) in terms of moose being the significant prey in the ecotype predator/prey system that they are at present. Hence, it is unlikely that any tendency toward a "normal" predator-prey equilibrium would have had time to "evolve".

Further, classifying a caribou herd as fitting the Alaska ecotype may largely be a function of herd size. For example, the Western Arctic Herd, numbering 342,000 in 1989, was subjectively excluded from the Alaska ecotype. However, if it numbered only 50,000 we would likely have included it in the Alaska ecotype. This observation illustrates that theory is not without its complications.

THEORY

If one concludes that caribou ecotypes are abstracts and not

substantive realities, then considering them as substantive realities would be termed reifying (Geist 1983). This is but one of several complications often encountered in the theory of caribou population dynamics. Geist (1983) identified ambiguous formulation of hypotheses (as did Bergerud 1980), semantic problems, and reifications as being systematic difficulties with population biology that preclude decisive testing of hypotheses. Much population dynamics theory, with management implications, revolves around and includes reifications. For example, we believe that carrying capacity is clearly not a substantive reality but is frequently perceived as such. Arguably, density-dependent population regulation may be a parallel. What additional complications confound our reaching collective understanding and agreement about limitation of caribou populations?

Certainly, caribou management in Alaska has erred in the past by applying general theory in lieu of specific knowledge, which is not unique to Alaska caribou management nor to caribou management alone.

Geist (1983) commented on a parallel regarding mountain goat management as had Smith (1980). "To substitute general theory for specific knowledge is very dangerous in wildlife management. The demise of mountain goats is in good part due to hunting seasons based on wrong population biology theory. Kuck (1977) showed how territoriality by female goats falsified the common assumption that compensatory reproduction follows increased mortality." In attempting to understand caribou population dynamics, both the general theory and specific knowledge, are we considering all possible or tenable hypotheses? Bergerud (e.g., 1980) has taken a leadership role during the past decade in identifying and testing high order hypotheses that relate to the underlying life history strategies of caribou (i.e., identifying ultimate limiting factors). Bergerud's focus in the past decade has been on "either-or" options between predation or food limitation hypotheses. Bergerud (1980) wrote that theoretically a food limitation exists but at much higher densities than are seen in the real world of observed values for herds free to disperse. In contrast, Bergerud (1980) concluded that, "Predation is considered the chief limiting factor to population growth and sets the level of stocking commonly at one to two animals per Mi² (0.4-0.8/km²) or less. Limits imposed by dispersion or food supplies occur at much higher densities."

We applaud Bergerud's (1980) leadership in focusing on hypothesis testing in caribou research and for emphasizing the utility of the hypothetico-deductive approach of the scientific method as follows:

"This review is an attempt at a synthesis. At the risk of error and oversimplification, I have always sought to elucidate common underlying properties and life history strategies between populations and subpopulations. I believe the scientific method is largely deductive (Hempel 1966, Platt 1964); that is that we hypothesize from the general to the specific that there is predictive power there. The

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plurality-ofcauses approach is self defeating. It provides no further synthesis or insight. An A <u>Posteriori</u> catalog of causes becomes descriptive and untestable. We proceed by hypothesis - we state what we will accept as disproof of our hypotheses so others can test them, disprove them, and formulate new hypotheses. By such a course we leave old ideas behind. Very clearly in North America in caribou research we have not followed the scientific method: hypotheses are seldom stated or tested; disproofs never mentioned. We have been descriptive and <u>ad hoc</u> and today we are wrestling with the same ideas as 25 years ago."

Bergerud's (1980) hypothetico-deductive approach to caribou research is clearly a good approach for identifying common underlying properties and life history strategies (i.e., ultimate limiting factors) as confirmed by Romesburg (1981). However, in the day-today business of the practical wildlife manager, identification of proximal (point in time) limiting factors may have practical management implications. And in the frame of reference of the wildlife manager, the plurality-of-causes approach may be relevant and practical.

We favor a plurality-of-causes hypothesis to explain what is limiting given caribou herds at any point in time. Bergerud (1980) argued that such an approach is self-defeating because it provides no further synthesis or insight. Again we believe Bergerud's argument was in the context of ultimate limiting factors, i.e.,

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"elucidating common underlying properties and life history strategies." We acknowledge that a plurality-of-causes approach can contribute to formulation of ambiguous hypotheses and may provide less predictive power, but it does not necessarily provide little insight or synthesis.

Peek and Eastman (1983) offered a "plurality-of-causes" type hypothesis for moose population limitation/regulation. We have modified it to serve as a discussion starter for a viable (testable?) and hopefully unambiguous hypothesis for caribou, as follows:

Factors which serve to limit/regulate caribou numbers in any population vary with population density and through time and space. Population growth (negative or positive) is determined by a variety of factors, such as predation, insects, disease, parasites, weather-snow conditions, and intraspecific competition interacting to affect births, deaths, and dispersal.

Peek and Eastman (1983) also reported approaching the subject of natural control of moose numbers through Poore's (1962, cited in Peek and Eastman 1983) method of "successive approximations." The method draws inferences from data and they are judged for validity as far as the data allow. Peek and Eastman (1983) observed that all hypotheses are flexible and subject to modification as new or contradictory evidence becomes available. Field investigations of large ungulates may best be considered in this light, since conclusive, refined evidence is not yet available. If this approach is valid, then induction may be a fruitful scientific approach. We contend that deduction can only follow induction. We believe there is merit/validity in both inductive and deductive approaches and that they need not be mutually exclusive.

In fact, we endorse the scientific approach advocated by R. May at the International Congress of Game Biologists in Norway in 1989 as presented to us by R. O. Stephenson (pers. commun.) as follows:

"Dr. May's point was that wildlife biologists spend too much time quarreling about the best methods when, in fact, we need to employ a wide range of approaches if we are to progress. These include long-term ("boring") monitoring, acute observation of natural history, observational and correlative field studies, natural experiments, manipulative experiments, as well as ideas and theory. These tools are equally important, and their application should be driven by a feel for the most appropriate method useful in dealing with a given problem."

Our closing comment regarding theory and its relevance to caribou population dynamics is about chaos theory. We make no pretense of understanding chaos theory and its relevance to caribou, but we believe there is compelling evidence that it may provide profound insight into existing unsatisfactory models of caribou population dynamics. As food for thought we have excised several short quotes

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from Gleick (1987) regarding chaos theory and its potential applicability to caribou population dynamics (Appendix A).



Fig. 4. The institutionalized framework for caribou management in Alaska.

MANAGEMENT IMPLICATIONS

What are the management implications of the general theory and specific knowledge available for caribou?. That of course depends on how accurate our knowledge is. Long overdue is evaluation of the progression, consistency, and validity of ideas, and data that have lead to our existing management programs. How clearly does any administrative jurisdiction transform scientific information into management practice? We attempt to graphically depict (Fig. 4) the stepdown process used in Alaska, as we see it, to get from theory and knowledge to management practice. Clearly, there is no institutionalized mechanism to assure that assessment and incorporation of new knowledge is timely.

We believe that an exhaustive, critical review is in order to clearly identify the valid ecological basis for caribou management. For example, does recognizing carrying capacity as a reification change its relevance as the foundation to base population size goals upon? Carrying capacity is only one of many confusing concepts (Dhondt 1988) that are central to the current theory and practice of caribou management.

LITERATURE CITED

Bergerud, A. T. 1978. Caribou. Pages 83-102 in J. L. Schmidt and D. L. Gilbert, eds. Big Game of North Alerica, Ecology and Management. Stackpole Books, Harrisburg, Pa. 494pp. . 1980. A review of population dynamics of caribou and wild reindeer in North America. Pages 556-581 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symp., Roros, Norway, 1979. Directoratet for vilt og ferskvannsfisk, Trondheim.

- Davis, J,L., R. Shideler and R.E. LeResche. 1978. Fortymile caribou herd studies. Alaska Dep. Fish and Game, Juneau, Fed. Aid in Wildl. Rest. Proj. W-17-6 and W-17-7. 153pp.
- Dhondt, A. A. 1988. Carrying capacity: a confusing concept. Acta Oecologica/Oecologia Generalis 9 (4) : 337-346.
- Doerr, J. 1980. Modeling the population decline of 2 Alaskan caribou herds. Pages 611-623 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symp., Roros, Norway, 1979.Directoratet for vilt og ferskvannsfisk, Trondheim.
- Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in Interior Alaska. Wildl. Monogr. 84. 50pp.
- Geist, V. 1983. On phenotypic reproductive strategies in mountain sheep and some criticisms of conventional population biology. Pages 82-92 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds. Symposium on natural regulation of wildlife populations. For. Wildl. and Range Exp. Sta. Univ. of Idaho, Moscow. Proc. No. 14. 225pp.

Gleick, J. 1987. Chaos. Viking Penguin Inc., New York. 352pp.

- Haber, G. C., and C. J. Walters. 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. Pages 645-663 in E. Reimers, E. Gaare, and S. Skjenneberg, eds. Proc. 2nd Int. Reindeer/Caribou Symposium, Roros, Norway, 1979. Directoratet for vilt og ferskvannsfisk, Trondheim.
- Hempel, C.G. 1966. Philosophy of natural science. Prentice-Hall, Englewood Cliffs, N.J. 116pp.
- Johnson, D. A. In press. Caribou survey-inventory activities 1989, Game Management Unit 9(D) and 10 (Unimak Island). Fed. Aid in Wildl. Rest. Ann. Rep. of Survey-Inventory Activities. Alaska Dep. Fish and Game. Juneau.
- Kuck, L. 1977. The impacts of hunting on Idaho's Pahsimeroi mountain goat herd. Pages 114-125, in Proc. First Internat. Mountain Goat Symp. (W. Samuel and.W.G. Macgregor, eds.). British Columbia Ministry of Recreation and Conserve, Victoria. 243pp.
- McCullough, D. R. 1979. The George Reserve Deer Herd. The University of Michigan Press, Ann Arbor. 271pp.

- Peek, J. M., and D. S. Eastman. 1983. Factors which naturally control moose populations. Pages 175-193 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds. Symposium on natural regulation of wildlife populations. For. Wildl. and Range Exp. Sta. Univ. of Idaho, Moscow. Proc. No. 14. 225pp.
- Pitcher, K. W., and D. A. Johnson. 1989. Investigation into causes of low calf recruitment in the Southern Alaska Peninsula Caribou Herd. Interim Report. Alaska Dep. Fish and Game. Anchorage. 11pp.
- Platt, J.R. 1964. Strong inference. Science 146:347353.
- Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. J. Wildl. Manage. 452:293-313.
- Skoog, R. 0. 1968. Ecology of the caribou (<u>Rangifer</u> <u>tarandus</u> <u>granti</u>) in Alaska. Ph.D. Thesis. Univ. of California, Berkeley. 699pp.
- Smith, B. L. 1980. Criteria for determining age and sex of American mountain goats in the field. J. Mammal. 69(2):395-402.
- VanBallenberghe, V. 1987. Effects of predation on moose numbers: A review of recent North American studies. Proc. 2nd Int. Moose Symp. Swedish Wildlife Research Supplement 1, Viltrevy. pp.431-460.
- Yesner, D. R. 1989. Moose hunters of the boreal forest? A reexamination of subsistence patterns in the western subarctic. Arctic 42(2):97-108.

Appendix A. Quotes regarding chaos theory excerpted from Gleick (1987).

Anyway, if the population kept bouncing back and forth, ecologists assumed that it was oscillating around some underlying equilibrium. The equilibrium was the important thing. It did not occur to the ecologists that there might be no equilibrium.

Textbooks showed students only the rare nonlinear systems that would give way to such techniques. They did not display sensitive dependence on initial conditions. Nonlinear systems with real chaos were rarely taught and rarely learned. When people stumbled across such things and people did all their training argued for dismissing them as aberrations.

Within ecology itself, as May saw it, a central controversy in the early 1970s dealt with the nature of population change Some read the message of the world to be orderly: populations are regulated and steady--with exceptions. Others read the opposite message: populations fluctuate erratically--with exceptions..... Those who believed that populations were steady argued that they must be regulated by some deterministic mechanisms. Those who believed that populations were erratic argued that they must be bounced around by unpredictable environmental factors, wiping out whatever deterministic signal might exist. Either deterministic mathematics produced steady behavior, or random external noise produced random behavior. That was the choice.

In the context of that debate, chaos brought an astonishing message: simple deterministic models could produce what looked like random behavior. The behavior actually had an exquisite fine structure, yet any piece of it seemed indistinguishable from noise.

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