

CARIBOU PROJECT SUMMARY AND REVIEW PART 2 - POPULATION DYNAMICS

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>1 Summary of parts 1 and 2

In part one of our review we concluded the following: 1. The interval between surveys should be increased to once every six years, the most efficient interval for detecting changes in population size. 2. Spring composition surveys on the Bluenose, Bathurst, Beverly, and Kaminuriak caribou herds should be continued annually. In part two of our review we discuss how GNWT research programs have contributed to our understanding of the ecological processes in the lichen-caribou-wolf ecosystem. We conclude that the biggest gap in our knowledge is how changes in wolf numbers relate to changes in caribou numbers and how food availability and wolf distribution affect caribou distribution and movements. We believe that future research should describe the timing and magnitude of changes in wolf numbers and how those changes effect caribou survival and population growth and distribution. This review attempts to link our knowledge of natural history to our understanding of ecological processes, to focus our thinking, and guide future research.

>2 Introduction

In Part 1 of this review we reasoned that now would be a good time to review past work and plan a long term approach to future studies. First, most caribou herds in the NWT were large and accessible to hunters. Second, many major research projects have recently ended. Finally, because we concluded in Part 1 that herd status can be adequately monitored with a longer interval between surveys, we now have the time and money to address other objectives. In Part 2 of this review we describe our understanding of the ecological relationships in the lichen-caribou-wolf ecosystem (LCWE) in relation to our past research results and outline our proposals for future research. We outline how regional plans can be integrated to an overall research program. Specific suggestions that might be useful for operational and planned projects being initiated by Regional Biologists are scattered throughout (e.g., our suggestion to Mike Ferguson that he collar at the Kouджуак River).

We considered 3 steps toward a thorough understanding of caribou ecology. The first step is to define the population, clearly a prerequisite to understanding population dynamics. The second step is to document caribou natural history e.g., litter size, age of first reproduction, diet, mortality rates, habitat use, behaviour, etc. The final step is to describe and quantify the key ecological processes i.e., those relationships that have the greatest effect on distribution and abundance; the numerical response of caribou to food availability, the functional response of wolf predation rates to caribou density, etc.

It is clear from this review that past GNWT research has made substantial contributions toward increasing our understanding of caribou ecology within those three areas. We hope that this review will provide a focus for people's thinking and improve planning of future research projects.

>3. Population definition

A caribou population is defined as a group of animals whose females calve in the same location each year (Thomas 1969). Techniques used to establish and test this definition have progressed from direct observation of caribou distribution and movements to ear tagging, VHF radio-collaring and satellite radio-collaring.

This definition appears to work fairly well for migratory barren-ground caribou, specifically the Bluenose, Beverly and Kaminuriak herds. Most cows return to the same area to calve each year and that place is distinct from calving areas used by cows from other herds (Heard and Stenhouse 1991, McLean unpublished). Both ear tagging and VHF radio-collaring have shown that fickle cows make up less than 5% of the population (Miller and Robertson 1967, Heard 1983, Heard and Stenhouse 1991). Those studies could not rule out the possibility that there are occasional movements between populations involving large numbers of animals as hypothesized by Skoog (1968). The large increase in the Kaminuriak herd between 1980 and 1982 (Heard 1981,

Gates 1985), if real, can only be interpreted as having resulted from massive immigration (Heard and Calef 1986).

The movements of radioed caribou showed that the original distinction between Melville, Wager and Lorillard caribou was unfounded (Calef and Heard 1980, Heard et al. 1981, Heard and Stenhouse 1991) because there was extensive interchange of cows among the three calving areas. We did not learn anything about the discreteness of the Queen Maud Gulf and Boothia caribou. Caribou throughout the region are for now considered one population, the Northeastern Mainland herd (Heard et al. 1983).

The results of satellite tracking of Victoria Island caribou are not yet available, but I understand that there are at least 3 separate calving areas. Apparently Gunn feels her data are now sufficient to allow her to monitor numerical changes, because she is terminating the project.

On south Baffin there are clearly both migratory and relatively sedentary caribou that have overlapping winter ranges. In addition, large numbers of caribou have calved in 'new' areas; almost certainly the result of changes in calving distribution rather than solely changes in numbers. (Decker, Donaldson, Ferguson pers comm). Further understanding depends on placing satellite collars on migratory caribou on the Koudjuak River.

Movements and herd discreteness of caribou on and around Boothia are largely unknown. Gunn's proposed satellite collaring program should provide enough data to design population monitoring surveys.

We see three problems with the population definition based on behaviour as proposed by Thomas (1969); caribou can have distinct calving grounds, but have overlapping winter ranges, caribou can share a calving ground, but have alternate life histories (e.g., taiga vs. tundra wintering) and caribou could disperse at calving and have no 'calving ground'.

If two herds use the same winter ranges, whether they use it at the same time or not, it may be impossible to allocate hunter kill etc. appropriately. This situation commonly occurs on Baffin Island and among all of the mainland herds. More intensive monitoring of movements would help solve the problem e.g., on Boothia Peninsula and vicinity.

There are tundra wintering caribou on what is normally the summer range of all of the migratory mainland herds. These animals probably calve on the closest calving grounds (e.g., cows wintering near Rankin calved at Kaminuriak Lake, Heard and Stenhouse 1991), but we did not learn anything about winter range fidelity. It is reasonable to assume that the population dynamics of tundra wintering caribou is different from taiga wintering animals. Studies in Alaska have clearly shown that there is no winter range fidelity. If the same is true in the NWT, then tundra and taiga wintering caribou are clearly all one population.

If caribou are dispersed at calving (e.g., woodland caribou, Peary caribou?, Banks?, Victoria?, south Baffin?) then strict application of the definition may lead to distinguishing an unreasonably large number of small populations. Certainly the Alaskans are recognizing more small herds occupying small areas as their knowledge grows. What we find unreasonable about recognizing many small herds is that they may draw attention (time and research money) away

from larger herds that more people depend on and ecological generalizations from small herds may be limited. For example, documentation of ecologically significant events such as 'massive' interchange of females between the Yanert and Delta herds in Alaska is not given much credit (with respect to Skoog's hypothesis) when it comes to its application to the larger herds. Conversely, if these small herds persist through time and the range use changes associated with changes in population size (i.e., they are not just a function of temporarily low density) then they should be recognized.

Satellite collars have three advantages over conventional VHF transmitters when addressing population definition questions. Satellite transmitters are the most cost effective technique when numerous relocation positions throughout the year are required, they provide data under all weather (flying) conditions, and relocation is independent of any preconceived ideas of where the animals should be. In practice, a mix of satellite and VHF collars would be the most efficient if large numbers of animals were to be marked because the satellite collars would make relocations of the VHF transmitters more efficient in winter when the animals are moving relatively little. We do not think more study on population definition is required over and above what is presently proposed and underway.

>4 Natural history

>4.1 Growth and reproduction

As with population definition questions, GNWT research projects have made a substantial contribution to our understanding of growth and reproduction (Adamczewski et al. 1987 and unpublished data from Rideout and Southampton islands).

Pregnancy rates in adults (3-year-old and older caribou) is always high, averaging 85% with most samples falling between 80 and 100% range but most are between 80 and 90% (review by Bergerud 1980, Parker 1981, Gates 1985, Messier et al. 1988, Thomas 1990, Heard unpublished data). Geist (1981) thinks migratory animals can maintain constant reproductive output because they roam over such large areas that the chance of finding adequate food is high. Another possible explanation is that the yield curve for lichen production has a sharp peak and can compensate over a wide range of grazing intensities. Regardless of the explanation the assumption is that summer food availability determines pregnancy rates.

There are a few data to examine the mechanisms that determine fertility. Most correlations between fat reserves and pregnancy rates are based on winter collections, when pregnancy is easily determined, but fat levels are not necessarily representative of October, when the 'decision' of whether or not to ovulate occurs. Ovulation is clearly related to fat reserves, but other factors are also important (Skogland 1990). Starving Rideout Island females did not ovulate. Fall fat levels on Southampton and Coats Islands were high and pregnancy rates were high, especially noticeable on Southampton Island where 100% of yearlings and 2-year-olds were pregnant. Fall fat reserves are important in determining ovulation and pregnancy rates but, on Southampton Island, fat reserves in calves were high but insufficient to result in pregnancy. Attaining a threshold body size is also

insufficient to explain the observed pregnancy rates because Southampton yearlings had higher pregnancy rates than Kaminuriak and Beverly 2-year-olds even though they were smaller.

The high pregnancy rates of all ages on Southampton Island demonstrates that reproducing early, e.g., as a yearling, does not necessarily prevent breeding the next year.

Because fall fat reserves influence ovulation, it seems reasonable to assume that summer nutrition is more important than winter food availability in determining pregnancy rates. Pregnancy rates appear to have declined along with the decline in summer food availability in the George River herd (Huot 1985, Messier 1989). On Coats Island, summer feeding conditions are excellent and pregnancy is high even though winter food availability is often severely restricted. Further support for the importance of summer nutrition comes from the fact that females do not appear to carry winter fat reserves through the summer (Clutton-Brock et al. 1982, Alley-Chan pers comm). Based on these arguments, we conclude that summer food availability in the mainland caribou herds limits pregnancy rates. Availability may not only be related to standing crop but may also be related to presence of predators and insects (Fig 5).

Growth rates, on the other hand, may at first appear to be related only to summer nutrition, because animals grow only in summer, but winter is also important. Summer food availability is high on both Southampton and Coats islands, but Southampton Island has considerably more winter food available and individuals are larger. Winter nutrition affects body size by directly influencing birth weights and birth dates (Adamczewski et al. 1987, Isle Royale moose, Skogland

* Also amount of time required to replenish depleted reserves may affect summer growth.

1990). Later birthing results in less time in summer in which to grow. Body size is important because survival is usually higher in larger individuals.

Changes in growth and reproduction within a population can be monitored most efficiently by examining young animals because they show a greater range in their response to food availability.

>4.2 Survival

No GNWT research projects have addressed survival rates directly. Our information is restricted to recruitment information, where sample sizes are large but inference is indirect (i.e., the change in ratio method) and the survival of radio-collared cows, where inference is direct but the sample sizes are small. Our data and data from elsewhere has convinced us that an understanding of survival rates is critical to understanding caribou ecology.

Survival, especially through the first year, is more variable and therefore probably more important than productivity in determining caribou population dynamics (Fowler 1981). Recruitment surveys indicate that survival has been much higher, about double, in the past 10 years of increasing caribou populations than in the previous 10 years when herds were declining (Heard and Calef 1986 and unpublished data). Males have lower survival rates than females and calves have lower survival rates than adults. Wolves and hunters are the primary caribou predators and on the calving ground surplus killing by wolves is common. We think first year survival is

between 25 and 50% and annual survival rates of adults is probably about 90% for females and 75% for males.

The high cost of measuring survival rates is the main reason why it has not been done in the NWT. To detect significant changes of adult or neonate survival rates requires intensive monitoring of many collars (e.g., 50-100 each year for several years).

Most calves that die are killed by wolves (Miller and Broughton 1974, Miller et al 1985) but adults are subject to both wolf predation and hunting. The number of caribou shot by hunters varies with availability i.e., caribou movements (Heard and Calef 1986). The GNWT coordinated a massive attempt to estimate hunting mortality through monthly interviews with hunters (e.g., Gamble, Donaldson, Jingfors). That technique was quite successful in some places but useless elsewhere. An alternative approach would be to measure mortality rates using radio-collared caribou. As previously mentioned, this would be an expensive operation but not in comparison to the interview program. The advantages over the interview approach would be that both hunting and natural mortality would be determined and any-biases would be more consistent across the NWT. The socio-economic disadvantages probably outweigh these advantages but at least we should recognize that there is a technique available to measure hunting mortality.

>4.3 Movements

The movements of caribou on the mainland is relatively well known on a gross scale e.g., most females arrive at treeline in September, winter in the forest, leave in April and arrive on their calving grounds by early June. Beyond those generalities a few key principles have emerged. The most important is that range use is density dependent. The amount of winter range used by the Kaminuriak and Bathurst herds has increased in conjunction with increases in herd size. Increased winter range use means that larger numbers of animals move into the forest earlier in the winter and go further south and west. The Kaminuriak herd has done this twice in the last 40 years with a substantial retraction during the intervening population low (Simmons et-al 1979, Heard and Calef 1986).

Summer movements are also affected. When the Kaminuriak herd was small, caribou no longer went to treeline in August where they had been tagged at a 'traditional' water crossing for many years (Miller and Russell 1972, Heard and Calef 1986, Heard and Williams submitted).

There are many ramifications to density dependent range use. First, in the absence of census data, we can assume that range expansion is a good index of population size e.g., Baffin Island. Second, increased penetration into the forest usually increases the availability of caribou to hunters and therefore more animals are shot. Third, with most wolf dens at treeline earlier arrival there may provide a basis for a functional response in wolves. (more on this later).

Thomas attempted to explain the effects of burns and snow depth on winter movements. Both appeared to effect caribou distribution and movements. Caribou appeared to use the eastern part of their range early in the winter before much snow has accumulated because snow is usually

deeper there than further west. Laurence Turney is examining the applicability of using GIS to evaluate if snow depths measured by satellites correlate with caribou distribution on the winter range.

In spite of the progress that has been made, the predictability of caribou movements is low. We believe that increased understanding of the causes of caribou movements would be valuable, would allow for refined management decisions in relation to hunting and land use practices/disturbance in addition to furthering our understanding of caribou ecology. Movements warrant further study as long as the techniques hold some promise of elucidating causation e.g., satellite collaring and remote sensing of snow depths and summer diet quality and body condition.

>4.4 Food availability and feeding behaviour

Except for Jingfors et al. (1982) and Adamczewski et al. (1988) information on caribou diets in the NWT has come from CWS studies (e.g., Thomas and Hervieux 1986, Miller 1972, Parker 1975). The dominance of lichens in the winter diet is typical but not universal (e.g., Coats and Banks islands) and has been confirmed by radio-caesium concentrations in caribou and wolf muscle.

>4.5 Predation

There is no doubt that wolf predation has a big effect on caribou numbers and behaviour even if or when the net effects are not limiting caribou population size. Wolves eat mainly caribou and caribou are eaten primarily by wolves (e.g., Heard and Williams carcass collections 1988-1990). In 1979 and 1980 we found selection for calves one spring but not the next. Conflicting data on age specific selection has been found by others as well. The best data come from Alaska where both Davis (pers comm) and Adams (1989) showed that selection for calves ended by fall but we feel that this subject is worth further study in the NWT. Miller and Broughton (1974) and Miller et al. (1988) and our own observations showed that surplus killing of neonates is common.

We demonstrated that winter predation rates based on radio-caesium are not as reliable as the direct estimates of kill rates by radio-collared animals. Fat levels in wolves suggest high predation rates on forested winter range but lower ones near Bathurst Inlet, thus predation is not the same on all winter ranges. Predation rates appears to be high enough to limit caribou numbers in some herds e.g., the Bathurst but not in others e.g., the George River herd.

>5 Ecological processes in the lichen-caribou-wolf ecosystem

>5.1 Ecological processes

The main thing that we are trying to understand about the ecological processes in the LCWE is; what forces determine and what forces regulate (i.e., change with caribou density) caribou numbers? Because population size is never constant in any species, it is more useful to

phrase that question as; what forces cause the LCWE to return toward equilibrium (i.e., dampen temporal variation) after the population size has been displaced from equilibrium? (Caughley et al. 1988:161 and 184). There may not be any regulatory forces if the population is limited by density-independent processes. A second question is; how do potentially density-independent forces, like summer weather and therefore insect severity and winter snow depth, affect the expression of density-dependent forces? Managing caribou requires the answer to those questions so that we know how to reduce the magnitude of population fluctuations.

In large mammals, density effects are most likely to occur near K (Fowler 1981) and we should expect to observe behavioural changes before demographic ones.

We use the phrase ecological processes as a synonym for what others may refer to as ecological relationships, functional ecology, or functional relationships; how ecological factors affect the way the ecosystem functions. Caughley (pers comm) pointed out that there were likely 5 main ecological processes in the LCWE:

- 1) The effect of weather on plant growth.
- 2) Caribou's food intake rate with respect to food availability (caribou's functional response). (Fig 1)
- 3) Caribou's rate of increase with respect to food availability (caribou's numerical response). (Fig 2)
- 4) Wolves' predation rate or caribou consumption with respect to caribou availability (wolves' functional response; probably type II). (Fig 3)

- 5) Wolves' rate of increase with respect to caribou availability (wolves' numerical response). (Fig 4)

Those relationships are general to all plant-herbivore-predator ecosystems but they have rarely been quantified (Caughley et al. 1988, Fryxell et al 1988). In addition to those five main relationships there are others that are specific to the LCWE (Fig 5), primarily those affecting the availability of food (to both caribou and wolves) rather than production.

The following section describes what ecological processes we think influence the functioning of the LCWE (Fig 5), how they operate, how past GNWT caribou research projects have contributed that understanding and where future research is most needed. The primary objective is to explain the influences on caribou numbers and distribution.

Steps 6, 7, and 16

The amount of food available is probably much lower than standing crop. Snow, bugs (warble flies and mosquitoes), and predators can reduce the food available to caribou in two ways; directly, by preventing caribou from feeding on food where they are at the time (steps 4, 5, 17) and indirectly, by causing animals to go elsewhere (steps 6, 7, 17). By definition, if those factors result in animals choosing to live elsewhere (e.g., in anti-predator/insect habitats) then those habitats are suboptimal for feeding (e.g., calving grounds). Displacement can also be local (e.g., cows avoiding riparian habitats that might hide wolves, or selecting insect relief habitat like snow and sand patches and shallow water). Direct food intake reduction occurs when animals are standing

on their food but are not able to feed as efficiently because 1) they have chosen to live in larger groups, to reduce insect harassment and predation risks, that intensify interference competition for food (Heard 1991), or 2) feeding time is being taken up by time scanning for predators or running to avoid bugs etc. Therefore, like snow, predators and insects can affect body condition, pregnancy rates, etc. through their effect on caribou behaviour.

Responses to changes in snow, predators, and bugs can occur over different time/space scales. Regional displacement is possibly an adaptive long term response e.g., going to calving grounds and possibly the east to west shift in the Beverly herd's winter range use but caribou begin to respond instantly to changes in bug densities and probably relatively quickly to changes in predation influenced group size.

Steps 8 and 16

Bergerud and Heard (submitted) showed that spring movements of males and females differed with males lagging behind on spring migration to take advantage of the earlier green-up of vegetation in the south. Females were on calving grounds where food was lower in quality because green-up was later. By late June the sexes were together and diet quality was indistinguishable. We suggest that wolf predation is responsible. Bulls choose better food, but take a higher predation risk, because wolves are more common further south (Heard and Williams submitted), to increase growth and therefore competitive ability in the rut. Females choose to forego better food by going to calving grounds (see also Eastland et al. 1989) in return for

increased likelihood that their calf will survive where there are fewer wolves (Table 1). On Southampton Island, where there are no wolves, sexual segregation occurs only locally and food eaten by both sexes is of equal quality.

Bergerud argues that caribou move around on the winter range simply to make it more difficult for wolves to find them. Regardless of what causes caribou to move around in winter their movements prevent wolves from establishing permanent territories because there are no alternative resident prey. This certainly alters wolf ecology (Heard, Fleck, and Calef unpublished). For example, where wolves live in stable packs within permanent territories only one female per pack reproduces each year. On migratory caribou ranges most females appear to breed each year (Heard and Williams 1989, Williams and Heard 1990, Williams 1991). There is still much to learn about the spatial association of wolves and caribou throughout the winter.

Sexual differences in feeding also occurs because the sexes differ in foraging efficiency. Sexual segregation is typical of all caribou and most other ungulates because the sexes have different energetic and reproductive strategies (see review by Main and Coblentz 1990). Foraging decisions involve trade-offs between food quality (protein and energy levels) and food quantity (available biomass). Males are expected to select areas with the highest quality food when availability is high everywhere like in late spring. Males may choose areas with lower quality and higher availability when availability is restricted (e.g., by snow and competition from dominant antlered females) and overall quality is low because their large relative body size enables them to use diets of lower quality. An understanding of the effect of feeding on sex specific distributional

differences could be important in assessing environmental disturbances (Jackimchuk et al 1987, Bergerud and Heard submitted) and encouraging hunters to hunt where males predominate.

Step 9

We suggest that it is unlikely that NWT herds will show a strong numerical response to food availability because densities are so low. Density-dependent resource limitation in Hardangividda (Skogland 1990) and the George River herd (Messier et al. 1988) occurred only at densities much higher than in NWT and Hardangividda range recovered at densities more typical of our high density herds (Skogland 1990).

Step 10

Ouellet is presently attempting to measure the effect of grazing on compensatory growth in lichens on Southampton Island. White et al. (1981) examined the functional response of caribou feeding in wet sedge habitat but there are no comparable data for caribou feeding on lichen.

steps 11, 12, 13, 14, 15, 16, and 17

Our thinking about steps 11 through 17 are linked together and our reasoning revolves around the key fact that most wolves den at treeline (Heard and Williams 1991). Messier et al. (1988) felt that wolf abundance must be independent of caribou density (step 14), and therefore

could not regulate caribou numbers (step 15), because pup survival is determined during the 4-5 month period when caribou migrate and are inaccessible to denning wolves. That could well be the case if wolves denned in the forest, but because we have shown that they do not den in the forest, caribou would not be inaccessible for the entire 4-5 month period when pups are sedentary.

Caribou availability to denning wolves is probably related to caribou density. First of all, the number of caribou that remain near treeline in July could depend on the number of caribou in the entire herd (step 12) but more importantly, because caribou show density dependent range expansion and contraction (Bergnerud et al 1984, Heard and Calef 1986, Valkenburg and Davis 1986, Messier et al 1988), more caribou should return earlier to the hunting range of treeline denning wolves as herd size increases (steps 11 and 13). When the Kaminuriak caribou herd was declining in the 1950's and 1960's it used less forested winter range in Manitoba and stopped going to treeline in late summer where caribou had been tagged for many years (Miller and Robertson 1967). In contrast, expansion of summer range by an increasing George River herd (Messier et al. 1988), has resulted in caribou reaching the trees in July, which is earlier than when the herd was smaller (Couturier et al. 1990).

The preponderance of wolf dens near treeline coupled with density dependent range use changes by caribou provides a mechanism for caribou densities to influence wolf numbers if recruitment of pups from treeline denning wolves influences wolf densities throughout the caribou range and if wolf recruitment is dependent on caribou availability (Heard and Calef 1986). The

concentration of dens near treeline suggests that production from those dens would have a major influence wolf numbers throughout the caribou's range, wolf pup survival appears to depend on the availability of caribou (Fuller 1989, Williams 1990), and wolf abundance appears to depend on pup survival (Van Ballenberghe and Mech 1975, Keith 1983). If the wolf numerical response is large enough then the potential exists for wolf predation to regulate caribou numbers.

Why do caribou show density-dependent range use changes and why do they move to treeline in the fall? Possibly they are driven by density-dependent competition for food. The George River herd fits this model by a) having poor and declining summer body condition and b) going to treeline earlier at higher densities. Summer food may be more abundant near treeline because caribou tend to avoid using it to reduce their predation risks. When caribou density increases they are forced to take greater risks to obtain sufficient food. Fall reductions in the nutrient content of summer foods (graminoids, forbs and shrubs) leaves lichen as the desired winter food. Lichen is most abundant in the forest. Caribou go to treeline but are reluctant to enter the forest until the lakes freeze in October when frozen lakes provide space to escape wolves.

Other facts support the rationale behind our reasoning. First, migration to calving grounds appears to be a successful anti-predator strategy for caribou because wolf densities are consistently lower on calving grounds than on winter ranges (Table 1). The location of the Beverly herd's calving ground before 1978, near a high density of wolf dens along the lower Thelon River, appeared to be inconsistent with the idea that caribou migrate to calving grounds to reduce predation on neonates. However, the Beverly herd has shifted calving areas northwards in recent

years. Some calving occurred south of the Thelon River and Beverly Lake in seven of eight surveys between 1957 and 1974 (Fleck and Gunn 1982) but all calving has occurred north of Beverly Lake, often far to the northeast, in all but one year between 1978 and 1988 and the number of wolves seen during calving ground surveys has declined from 887/1000hr (mean of three surveys) between 1971 and 1978 to 143/1000hr (mean of six surveys) between 1979 and 1988.

Second, if the primary reason for going to calving grounds were to avoid denning wolves rather than unencumbered ones then we would expect calving ground locations to be as unpredictable as caribou movements at all other times of the year. However, we find just the opposite; calving ground locations are the most predictable aspect of caribou life history. Presumably predicability helps to concentrate calving cows and, along with calving synchrony, improves calf survival by swamping the few wolves that do remain associated with cows over the calving period.

Third, relative to the other three caribou herd ranges, we found a higher proportion of Kaminuriak range dens on the tundra. This is consistent with the changes in Kaminuriak caribou distribution that occurred during the 1970's and 80's. That is, as caribou numbers decline the herd avoids moving to treeline, wolf pups starve and more may attempt to den on the tundra near the calving ground. One reason wolf numbers may have declined is that this strategy was not as effective i.e., pup survival was not as high as it had been at dens near treeline, and wolves showed a numerical response to changing caribou densities. This explanation is consistent with risk

sensitive foraging theories (Real and Caraco 1986). When caribou return relatively predictably to treeline, wolves pursue a risk-averse strategy by denning there. When caribou fail to return, wolves are forced into a risk-prone approach by denning on the tundra where caribou availability is less predictable. Conversely, when densities are low caribou are relatively risk-averse by avoiding treeline. When caribou densities increase and food availability declines they go to treeline earlier, a risk-prone strategy.

Our model of the LCWE describes a mechanism for Bergerud's (1980, 1983) caribou population regulation hypothesis and expands on the points presented by Heard and Calef (1986). Wolf dens are concentrated at treeline, the availability of caribou to denning wolves is a function of caribou densities, and wolves show a numerical response to caribou availability. The system alternates between states when the caribou are responding behaviorally to predation pressure [spacing away] and when they are responding to intraspecific food competition [going to the treeline earlier in summer].

Fryxell et al. (1988) showed ungulate migrations in Africa can allow ungulates to become numerous because they can escape predators until they are eventually limited by food. Messier et al. (1988) proposed a similar explanation of density-dependent food limitation in the George River herd because caribou population growth did not produce a regulating numerical response in wolves.

The George River herd data cannot be used to refute the multiple equilibria model proposed by Haber and Walters (1980). This hypothesis suggests that wolves can regulate caribou

numbers only at low densities (like we have in the NWT) but wolves cannot catch caribou herds that break out of the dreaded 'predator pit' before growth is stopped by density-dependent food limitation.

>5.2 The implications to management

Understanding caribou ecology is essential both to actively manage caribou and to predict trends in caribou numbers. We do relatively little manipulative management now but with increased demands and responsibilities associated with the settlement of land claims, we can expect increased management demands. Because no population is ever stable for long but will change with natural and man-induced perturbations (e.g., weather, disturbance from resource development and tourism, fire, etc), it is important to predict trends and, if action is necessary or possible, prescribe the proper remedial action. If there is support for manipulative action, one needs to know what variables to manipulate and how to change them to reach an objective and what kind and rate of response to expect. The ability to predict trends is important even if we do not expect to be able to effect them so that people will be prepared for the future. A better understanding of caribou ecology would increase the likelihood that management recommendations could be conceived that would be acceptable to everyone.

>6 Research proposals

We hope to carry out new projects 1, 2, and 3 as a combined ecological study because they represent the best combination of the most pressing issues that can be addressed adequately with the money available and have the potential to result in management recommendations. We have also listed 4 others projects that we consider worth attention given sufficient time and money.

1 - Functional and numerical response of wolves to changing caribou densities.

For wolf predation to have the potential to regulate caribou numbers wolf predation rates must be related to caribou density. If wolf abundance depends on caribou density the mechanism is probably that pup survival is determined during the summer when caribou may be inaccessible to denning wolves. Because most wolves den at treeline, caribou would rarely be inaccessible to treeline denning wolves for the entire 4-5 month period when pups are sedentary, but accessibility could depend on caribou density. The number of caribou that remain near treeline in July could depend on the number of caribou in the entire herd, and, because caribou show density dependent range expansion and contraction, more caribou might return earlier to the hunting range of treeline denning wolves as herd size increases.

This study will examine the dependence of wolf pup survival on caribou density and predation rate. In addition, because caribou abundance will vary widely over the summer, this study will determine the functional response of wolves i.e., the change in predation rate with caribou density. Wolves will be radio-collared at 2 dens and tracked intensively for 4 weekly intervals to determine pup survival, predation rate on caribou and prey selection. In the fall 2

wolves and 2 caribou will be captured and fitted with satellite collars to track throughout the winter and to compare movements and determine winter predation rate and prey selection. In the second year the same type of work will be done but one of the two dens will be on the calving ground (possibly the Beverly herd's?) so that predation rates on neonates can be calculated.

Throughout this work we will attempt to see how we can apply the results to wolf census methods or abundance indices (e.g., den occupancy, carcass discovery times, howling) and tested by supplemental feeding experiments. We will do more den searches whenever possible (e.g., on the Elk River).

Understanding the effect of wolf ecology on caribou population dynamics need not lead to prescriptions for wolf reduction. Our mandate is to manage caribou and that can only be done if we have an accurate understanding of caribou ecology. As S.J. Gould said, 'Scientific truth, as we understand it, must be our primary criterion. We live with several unpleasant biological truths, death being the most undeniable and ineluctable.' If wolves suppress caribou numbers and prevent their increase we will learn to live with that fact as well.

2 - Circannual changes in Bathurst body condition and summer habitat quality.

This study will coincide with part of Ray Case's thesis research (Adaptations to prolonged periods of low nutrition in northern ruminants). It will extend the summer work we began last year on fecal Nitrogen, and will provide data to compare the body composition and movement rates of Bathurst animals with those from the Porcupine and George River herds. It will include

periodic collections of a few animals throughout the year, snow urine and summer feces from animals associated with 2 or more satellite collared caribou. We would also attempt to evaluate behavioural indices with range conditions (e.g., Derek's pride and joy: steps and bites / minute).

3 - Caribou movements in relation to snow depth

This is a test of Don Thomas's work using satellite imagery and will be Laurence Turney's thesis topic. We have already begun examining imagery and plan on collecting a few more snow measures this March. The technique works but needs to be fine tuned for our forest types, snow densities, and lake densities. Secondly we will test Thomas' generalization that snow accumulation on the Beverly range is usually greater in the east than the west. Our third objective will test the hypothesis that caribou move to avoid snow over 60cm deep. Fourth, we will reanalyse and quantify Thomas' data on the combined effects of snow depth and fire on winter caribou movements. Fifth, we will gather new information on caribou movements by tracking satellite radioed caribou (possibly both Bluenose and Bathurst) to test our ability to predict caribou movements. Sixth, we will correlate our calf cow ratios for past surveys on all herds and in all years to see how they relate to snow depth and the timing of snow deposition. Seventh, we will relate Peter's predation rates to snow depth. Finally, we will relate snow depth to Ray Case's body condition data.

4- Limiting factors in the caribou/muskox/wolf ecosystem; Banks Island

The importance of wolf predation to caribou recovery on Banks and in general to multiprey situations (e.g., with moose and bison in the Mackenzie Bison Sanctuary) is likely critical. Collar wolves and study prey selection in summer. Collar caribou to study calf survival or at the least expand caribou composition counts to late June when both calves and yearlings can be identified. Carry out wolf den observations and scat collections. Compare Banks to Melville and Prince of Wales and be part of the 'bison ecosystem' study.

5 - Compare feeding ecology and range conditions in overgrazed and lightly grazed areas of Fox Peninsula to Southampton Island.

6 - Calf growth and survival from birth to age one

We would collar calves in fall or June (if we could afford it) and monitor for mortalities. We would examine fecal N vs distribution and calf growth vs calving time and location e.g., early vs late and central vs peripheral

7 - Adult mortality rates

Other - Host a modelling workshop (with Fryxell?) to screen for credible hypotheses and sensitivity analysis (i.e., the necessary magnitude for significant change, Walters 1986:82, Walters and Holling 1990)

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>8 Appendices

>8.1 Publications resulting from our review year

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Bergerud, A.T. and D.C. Heard. Spring migration and the importance of calving grounds to barren-ground caribou. (OIKOS)

Heard, D.C., J. Ouellet, and L. Gray. Growth of an introduced caribou population on Southampton Island, Northwest Territories.

Williams, T.M., D.C. Heard and K.G. Poole. Population dynamics of the Beverly caribou herd, 1971-1989

Manuscripts prepared for conference presentations or internal use

Bullock, S.J., T.M. Williams, and D.C. Heard. Do wolves (*Canis lupus*) move pups when dens are approached by people?

Heard, D.C. and L. Gray. The use of a random block survey technique to estimate caribou numbers on Southampton Island, Northwest Territories in 1987. Heard, D.C., and T.M. Williams. The 1986 Bathurst calving ground census.

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Heard, D.C., and T.M. Williams. The beauty of pollution: Estimating wolf consumption rates from radiocesium concentrations in wolves and their prey.

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>8.2 1990 Strategic Plan Submission

2. Caribou

a. Rationale

Caribou are the most valuable renewable resource in the NWT. They have not only tangible and measurable value as both a domestic and commercial meat source, but also intangible value as an integral part of native culture and as a symbol of northern wilderness for tourists. In most parts of the NWT, caribou are abundant and accessible to hunters but caribou numbers and availability are below expectations in some areas like Banks Island, throughout the High Arctic, and near Fort Smith.

Caribou research projects can be classified into one of three main areas; population definition, population monitoring, and population dynamics. All three of these areas of study provide information necessary to manage caribou. Population definition is a necessary precursor to any monitoring or management action. Herd size cannot be determined if we have no way of knowing what constitutes a herd or to which herd hunter kill or recruitment estimates should be assigned when herd ranges overlap, as they occasionally do in winter. In the course of defining population boundaries other important life history characteristics like calving locations are also discovered.

Monitoring population size is the best way to keep track of herd status. Annual recruitment estimates, based on herd composition in spring, are good indicators of population growth rate in the years between censuses. It may be necessary, in some circumstances, to use other population attributes like distribution, fecundity, body size and condition, sex ratio, environmental and range conditions, but they are clearly one step removed from our primary objective. Census and recruitment surveys have been the primary emphasis of the caribou program in the past but, because most herds are presently large and meeting people's needs, monitoring intensity can be reduced.

For most parts of the NWT there is more information available on population definition and population status than there is on population dynamics. Understanding the key ecological factors and processes influencing population dynamics is critical if we are to refine caribou management or predict the availability and abundance of caribou. The need to increase our broad ecological understanding is recognized within the Wildlife Management Division of the DRR and it is recognized in the Beverly-Kaminuriak, Bathurst, Banks Island and Porcupine caribou management plans or draft plans. Now, when herds are large, is the time to do that work. Unlike monitoring data, the results of research into ecological processes do not become dated and knowledge is cumulative. Understanding caribou ecology will reduce our uncertainty about current management

policies and will provide better predictions of future population changes either in the presence or absence of management action. As land claims are settled and co-operative management boards formed, it is likely that demands on caribou will increase but there will be public support for tough management decisions. Attempting controversial management approaches in the absence of data may preclude public support for potentially successful management programs, jeopardizing both the resource and benefits to users. Finally, any reliable assessment of the impact of industrial/resource development on the behaviour and ecology of caribou is contingent upon an understanding of how the ecosystem operates in the absence of those impacts.

I am advocating the need for research into ecological processes, 'But we must not pretend that process research and diligent data analysis alone will provide answers that resource managers can trust.' (Walters and Holling 1990:2066). Renewable resource policy and management requires information not only from research into population definition, population monitoring, and the ecological factors influencing population dynamics but also from experimental management programs or adaptive management (Walters 1986, Walters and Holling 1990) e.g., Gasaway et al. (1983, 1990). We are doing relatively little in this final area of research because an understanding of ecological processes is a critical antecedent to the use of adaptive management.

b. Major emphases

Population definition remains the major emphasis in the Kitikmeot and Baffin Regions. On southern Baffin Island it is clear that movements vary among sub-populations and have changed with time. In 1991/92 emphasis will be placed on collaring animals in the migratory sub-population (i.e., the animals that calve north of Nettling L and winter around various south Baffin communities). Study results will allow the hunter kill to be apportioned among sub-populations.

Annual recruitment surveys are planned for the Banks Island, Bluencose, Bathurst, Beverly, and Kamiruriak herds. Censuses are planned for Banks and Southampton Islands and the Bluencose herd. The last censuses on the Bluencose herd and Southampton Island were in 1987 and on Banks in 1989. Part one of the caribou project review argues for 5 or 6 year survey intervals in future but the Bluencose and Southampton Island censuses were planned before that paper was written. The Banks census is justified because numbers are so low and possibly still declining.

Ecological processes that can ultimately affect caribou numbers are being studied on Banks, Victoria, and Southampton Islands. Body condition studies on those three islands will determine the effect of food availability, as measured through seasonal changes in fat reserves, on fecundity and the probability of starvation. On Banks Island, studies will examine the prevalence of disease and measure food use and production. On Southampton Island, the influence of grazing on lichen production is being measured through the use of fenced feeding exclosures and clipping experiments.

A management plan for Southampton Island caribou will be based on our research into population definition, population monitoring, population dynamics, local knowledge, and community consultation and could be considered a first attempt at adaptive management of caribou in the NWT.

c. Annual costs

Sub-project	1990/91	1991/92	1992/93	Source
S Baffin collaring	115	115	115	Baf
N Baffin collaring	1	1	1	Baf
NE Victoria Is herd identity	35			Kit
Bluenose census		35	50	IIF
Southampton/Coats census		45		HQ
		10		Kee
Banks census**	35	53	14	IIF
Spring composition				
- Bluenose herd	38	42		IIF
- Bathurst herd	20	20	20	HQ
- Beverly herd	20	20	20	HQ
- Kamiruriak	8	8	8	Kee
Bluenose body condition		2	2	IIF
Banks body condition and herd composition**	67	19	55	IIF
Porcupine body composition	10	10	10	Inv
Baffin body condition study	5	5	5	Baf
Baffin disease	1	1	1	Baf
Southampton feeding ecology	10	10	5	HQ
	10	10	5	Kee
Banks winter feeding**	15	43	31	IIF
Banks disease research**	18	35	18	IIF
Victoria Is caribou ecology	10	14	15	Kit
	5	7	42	IIF
HQ Travel and general equipment	24	24	24	HQ*

** in conjunction with same objective for muskox

* regional costs for travel and general equipment are not included here

d. Proposed new initiatives.

The proposed caribou ecology study will increase our understanding the key ecological factors necessary to manage and predict the availability and abundance of caribou. This study will examine density-dependent processes, i.e., those forces that cause caribou numbers to decline when densities are high and the changes that occur in those factors that allow caribou numbers to increase when densities are low. The approach will be to compare the relative effects and interactions between food availability and wolf predation in caribou populations existing at different densities; the medium density Bathurst and Beverly herds, the high density George River herd (GRH) and the low density Porcupine caribou herd (PCH). Moreover, we will compare caribou populations with different wolf densities, the ecology of males, females and immatures within the Bathurst and Beverly herds. Body composition studies on the GRH and PCH have shown big differences in the annual cycle of fat and protein accumulation and catabolism. Those differences may be related to density or habitat characteristics. The Bathurst herd range is generally like the PCH and densities are closer to the GRH. Densities in the Beverly herd are lower. We also plan to test hypotheses concerning wolf behaviour and production in response to changes in caribou densities and caribou behaviour by intensive monitoring of wolves. Some comparable wolf predation data is also available from both the PCH and the Bluenose herd (also a low density population) but we would examine some more specific questions e.g., about pup production and survival in relation to caribou movements. We believe that it is more efficient to learn about caribou mortality by studying wolves than by studying (collaring) caribou. Studies in the Keewatin, Alaska, the PCH and the GRH demonstrate that hundreds of collared caribou-years and hundreds of helicopter hours are needed to determine mortality rates whereas prey selection and predation rates can be estimated more quickly and easily by following wolves. It is possible that the Keewatin Regional Biologist will examine the effect of wolf densities by comparing caribou body composition, feeding behaviour and food availability between Southampton where there are no wolves and the Kaminiuriak range where there are few wolves or the Beverly range where wolves are abundant. Collaring a small number of both sexes of caribou would be required to examine movements and movement rates in relation to snow depth, spring melt, wolf movements, fire history, caribou density (relative to other herds), wolf dens etc.

On Banks Island, both caribou and muskox will be collared with satellite transmitters to describe calving and feeding areas and to determine overlap in winter range use between the species.

The objective of the caribou condition study, using frozen urine samples collected from the snow, is to examine the physiology of fat and protein catabolism when food is restricted and determine if indicators of protein breakdown are present in caribou urine. If so, then the collection of urine from the snow will provide a cheap and reliable way to assess changes in body condition throughout a population. This could be a useful annual monitoring tool where we can not afford the time or money to measure fat reserves on shot animals and where animals are rare and large numbers of shot animals are not available for a direct examination of body condition.

Snow depth restricts food availability and influences caribou distribution and movements, and therefore indirectly affects both their survival and their availability to hunters. It appears that snow depth can be determined from satellite imagery. This study will evaluate the accuracy of snow depth measures determined by satellite sensors. Positive results will be used in the GIS to evaluate caribou movements in relation to snow depth and fire history.

In the Kitikmeot Region, satellite collaring proved effective at documenting herd movements on Victoria Island and will now be attempted in the Pelly Bay area. Collaring near Pelly Bay will not only determine how to allocate the hunter kill but also assist in the design of censuses to monitor trends in herd size.

In the Baffin Region, range conditions on the Foxe Peninsula appear to have changed drastically over the past 10 years. Documentation of the present range conditions in comparison to relatively nearby and ungrazed Southampton Island may provide insights into the underlying causes of changes in caribou distribution.

e. Annual costs of new initiatives

Sub-project	1990/91	1991/92	1992/93	Source
Caribou ecology		95	135	HQ
		12	27	Kee
Banks behaviour studies**	142	37		IIF
Banks habitat analysis**	14	7		IIF
Banks technician**	55	54		IIF
Urine/condition		4	4	HQ
		9	9	HQ-215
Remote snow depth measures		5	5	HQ
Pelly collaring	60	60		Kit
Foxe Peninsula range study	25	25		?

** in conjunction with same objective for muskox
 ? Greg Henry, University of Alberta

12. Wolves

a. Rationale

Wolves are an important furbearer in the NWT, but the main reason for establishing wolf research projects is because wolf predation profoundly effects on caribou behaviour and population dynamics. Where wolves prey on migratory caribou, wolf behaviour is substantially different from wolves elsewhere. How wolves respond to changing caribou numbers is a key factor in caribou population dynamics. We are gradually building up a picture of wolf natural history, what we need to know now are the factors that influence wolf abundance.

b. Major emphases

The major wolf research project is the behaviour study on the Bluerose caribou herd's range. The objectives of that study are to determine wolf movements throughout the year and to describe wolf social organization, food habits, predation rates and productivity. All the carcass collections provide data on the basic biology of wolves such as food habits, body size, growth rates, annual cycle of fat deposition, litter size and reproductive history, and population composition.

c. Annual costs

Sub-project	1990/91	1991/92	1992/93	Source
Carcass collections: Bathurst and Beverly caribou ranges	7	7	7	HQ
Behaviour study: Bluenose caribou range	94	73	73	IIF
Carcass collection: Bluenose caribou range	2	2	2	IIF
Carcass collection: Banks Is	4	4	4	IIF

d. Proposed new initiatives

There is a pressing need to evaluate the role of wolves in the decline of caribou on Banks Island now, not in 1994/95 as requested in IIF.

Laurie,

25/2/91

Derek wanted me to add a separate strategic plan listing for this project under the wolf heading. Allocate 45K per year 1991/92 and 1992/93 and subtract the same from the caribou ecology study.

d. Proposed new initiatives - Functional and numerical response of wolves to changing caribou densities.

For wolf predation to regulate caribou numbers wolf predation rates must be related to caribou density. If wolf abundance depends on caribou density the mechanism is probably that pup survival is determined during the summer when caribou may be inaccessible to denning wolves. Because most wolves den at treeline, caribou would rarely be inaccessible to treeline denning wolves for the entire 4-5 month period when pups are sedentary, but accessibility could depend on caribou density. The number of caribou that remain near treeline in July could depend on the number of caribou in the entire herd, and, because caribou show density dependent range expansion and contraction, more caribou might return earlier to the hunting range of treeline denning wolves as herd size increases.

This study will examine the dependence of wolf pup survival on caribou density and predation rate. In addition, because caribou abundance will vary widely over the summer, this study will determine the functional response of wolves i.e., the change in predation rate with

caribou density. Wolves will be radio-collared at 2 dens and tracked intensively for 4 weekly intervals to determine pup survival, predation rate on caribou and prey selection. In the fall 2 wolves will be recaptured and fitted with satellite collars to track throughout the winter and compare with caribou movements and determine winter predation rate and prey selection for comparison.

e. Annual costs of new initiatives

Total strategic plan budgets [not submitted with plan]

ongoing caribou subtotals	119	79	HQ	
		247	204	IIF
		14	15	Kit
		28	13	Kee
		122	122	Baf
		10	10	Inv
		—	—	
		540	433	
new caribou subtotals	104	144	HQ	
		9	9	HQ-215
		211	98	IIF
		60	60	Kit
		12	27	Kee
		—	—	
		421	363	
wolf subtotals	7	7	HQ	
		79	79	IIF
all; subtotals by area	230	230	HQ	
		9	9	HQ-215
		537	381	IIF
		74	75	Kit
		40	40	Kee
		122	122	Baf
		10	10	Inv
		—	—	
Totals	1022	867		

>9 Table 1. Relative wolf densities based on the number of wolves seen per thousand hours of aerial survey flown over the ranges of the four mainland barren-ground caribou herds (from Heard and Calef 1986, Heard 1991, Heard and Williams submitted, Bergerud and Heard submitted).

Herd	Winter range (hr)	Calving ground (hr*)	Summer range (hr)
Bluenose	480 (303)	10 (200)	170 (47)
Bathurst	1070 (342)	80 (500)	
Beverly	1200 (546)	490 (350)	285 (186)
Kamirauriak	700 (589)	60 (400)	

* We assumed that 50 hours were flown each year a calving ground census was carried out

>10 Figures

General ecological relationships in the lichen-caribou-wolf ecosystem.

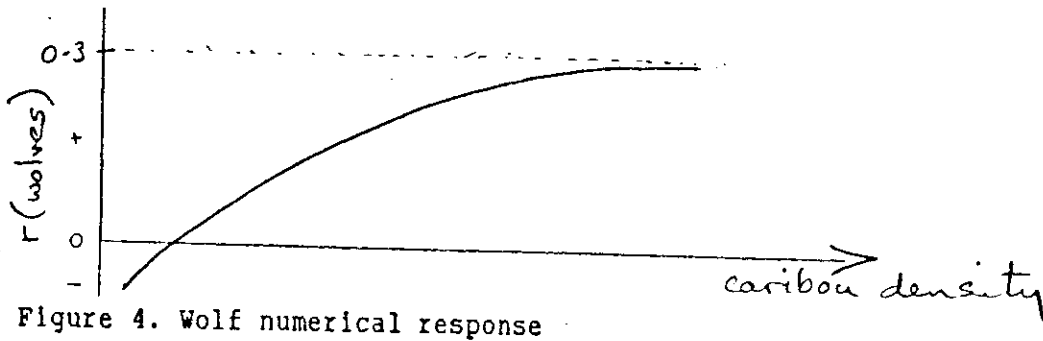
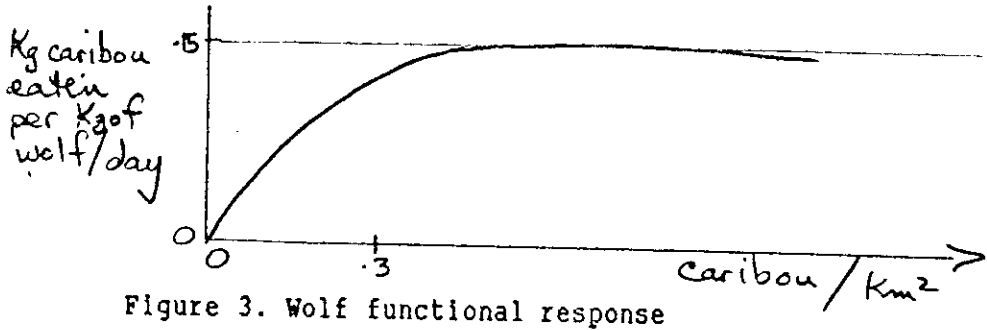
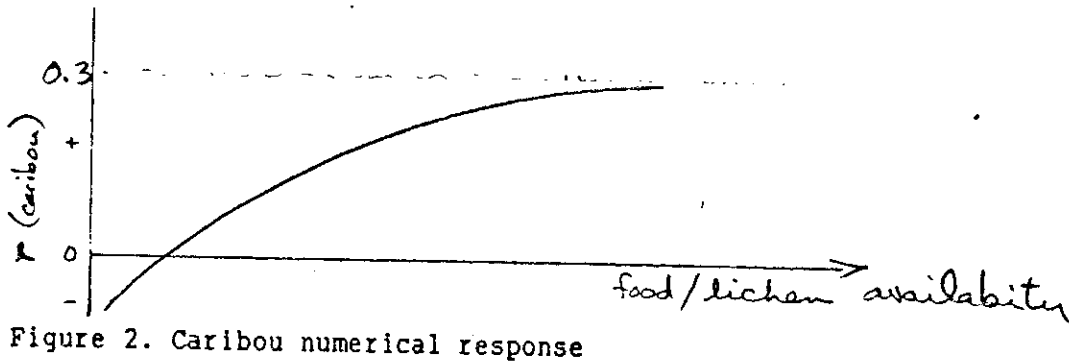
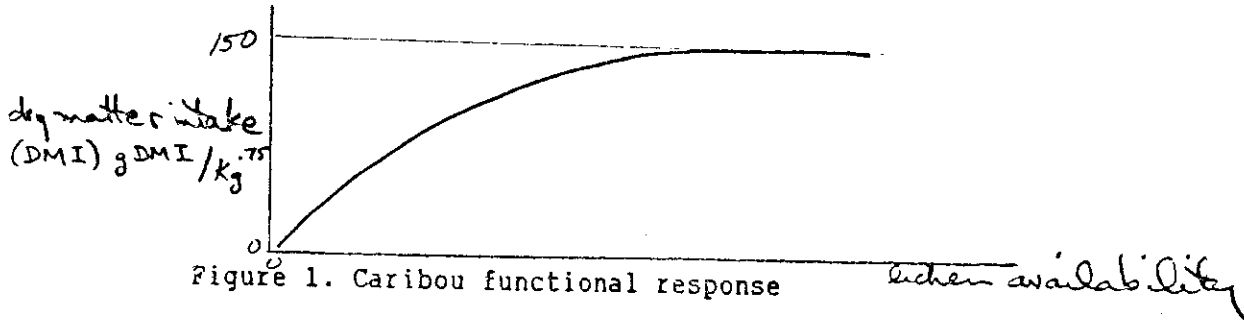
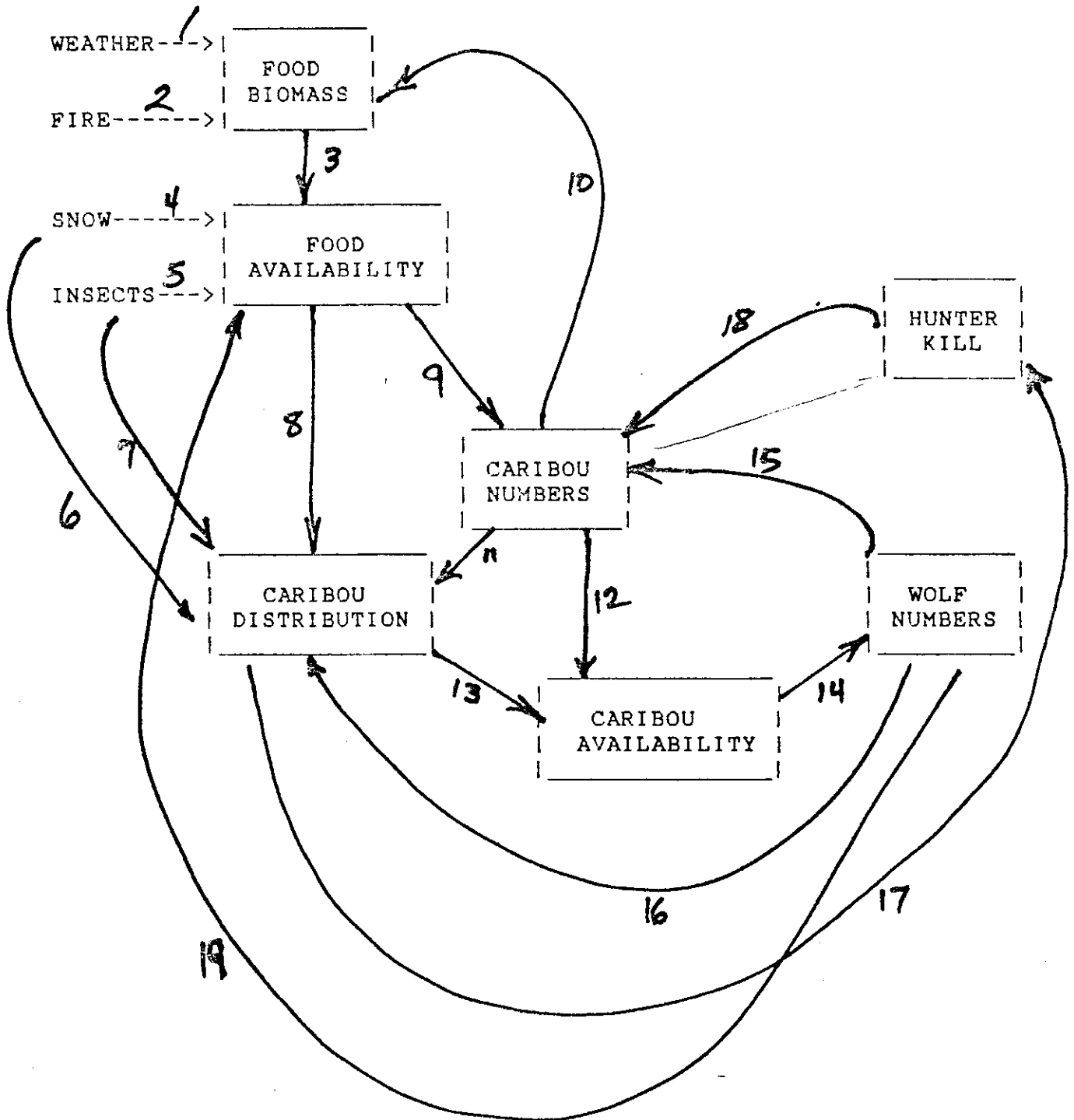


Figure 5. Ecological processes affecting caribou distribution and abundance



Biologist Meeting March 1991

Heard and Williams: Summary of Caribou Project Review

Calf cow ratios in spring are worth collecting because they can be used to support less frequent census surveys (e.g., George River, Kaminuriak, Beverly, Southampton Island populations) and indicate adult mortality (Bergerud TREE 1988). However, there would be a problem if they were not correlated. We had good recruitment and a decline, (non-significant) in estimated size in the Bathurst herd between 1986 & 1990. We used recruitment to argue there is no reason to predict a further decline. But is this logical? The same problem exists with other non-census data, e.g. fat levels, pregnancy rates etc.

The only reason to change our recommended survey interval from 6 years is if precision changed. Thus Baffin could go to something longer, say 1 every 10 years. Trend implies that a survey is repeatable even if it is inaccurate. Absolute estimates are not essential at the level of intensity with which we manage. We should try to improve repeatability if we go to a longer (6-10 year) survey interval but how we can do that without almost doubling the already high costs? Ideas?

We concluded that the key to whether caribou are limited by food or predation is whether or not caribou can escape wolves, i.e., does migration prevent wolves from showing a numerical response (pup survival) to changing caribou densities. If wolves do not show a numerical response then predation cannot regulate caribou numbers but the presence of a wolf numerical response is insufficient to conclude that predation is regulatory. Mark's data suggests that pup survival is related to caribou densities (but more data are needed) but it has yet to be demonstrated that caribou abundance at treeline density-dependent. Migration still functions as an anti-predator strategy (e.g. cows going to calving grounds) but it may not be completely successful. Sexes differ in their predator risk-food reward strategies with bulls risking more in early summer for good food as demonstrated by fecal nitrogen samples. Predators (and bugs) can have non-lethal effects on energetics by altering distribution and foraging efficiency (e.g. group size).

Summer is clearly an important time ecologically influencing growth, pregnancy and survival. Radiocesium shows that in some areas (e.g. the Richardson mountains) caribou not eating lichens. Cesium concentration is a poor estimator of caribou consumption rates by wolves.

The 3 key research (null) hypotheses are:

1. There is no correlation between wolf predation rates and caribou density at treeline dens during summer, i.e., when caribou density declines because of migratory movements wolves can still find enough caribou so that kill rate remains at same rate as in winter.
2. Summer wolf pup survival is independent of predation rate on caribou.
3. Caribou migration in summer does not improve access to food of higher quality or quantity.

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Heard: What Constitutes Caribou Management?

Management is some action that alters caribou ecology (e.g. distribution or abundance). Actions can be directed toward people (e.g. hunting quota changes) or other environmental influences (e.g. fire suppression). Surveys and board meetings do not constitute management, nor is simply forecasting a decline unless we expect people to change their hunting behaviour in response to that prediction. Given that all populations fluctuate, I think a reasonable management objective is to reduce the amplitude of fluctuations as much as possible and secondarily to influence the mean herd size.

Caribou management actions in the NWT are rare compared to most other jurisdictions. Southampton Island is an exception. I propose to eliminate hunting restrictions there, in hope people will shoot the entire annual recruitment keep the herd well below hypothetical K. If the herd declines, reducing the number shot should allow rapid recovery as range should remain in good shape. If the herd continues to increase the rate it approaches K will be much reduced, minimizing subsequent overshoot and decline. Active introduction of wolves is an unpopular suggestion, but may happen naturally.

On Banks and in the high arctic there are few options. Even if wolves are a problem, hunter kill must be reduced now.

Bathurst herd has many strong and conflicting interests and complex ecology. Conflicting demands allows for creative solutions e.g. complex quotas if ecology is understood.