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Proceedings of the Fifth American Caribou Workshop, Yellowknife, Northwest Territories, Canada, 19-21 March, 1991

RANGIFER

Scientific Journal of Reindeer and Reindeer Husbandry

Special Issue No. 7, 1991

Rangifer
Published by: Nordisk Organ for Reinforskning (NOR) Nordic Council for Reindeer Research.

Editor: Sven Skjenneberg
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Bank account: 4760 56 92776
Postal account: 2 11 63 58

Subscription prices:
Ordinary subscription, prices/year:

Nordic countries	NOK 70,–
Europe, surface mail	NOK 80,–
Europe, air mail	NOK 125,–
Oversea, surface mail	NOK 85,–
Oversea, air mail	NOK 170,–

Back issues:

Ordinary issues	NOK 15,– per number + postage expenditures
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NOK 250,– + postage expenditures.
Proceedings of the Fifth International Reindeer/Caribou Symposium:
NOK 200,– + postage expenditures.

ISSN 0801-6399

A/S Harstad Tidendes trykkeri

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Special Issue No. 7

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Proceedings of
the Fifth North American
Caribou Workshop
Yellowknife, Northwest Territories
Canada, 19–21 March 1991

Editors:

Doug Heard and *Mark Williams*

Published by: Nordic Council for Reindeer Research (NOR)

Harstad, Norway, 1991

RANGIFER

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Acknowledgements

Sponsors:	Government of the Northwest Territories, Department of Renewable Resources, Yellowknife. Air Tindi Limited, Yellowknife.
Organizing committee:	Bob Bromley, Ray Case, Derek Melton, Laurence Turney, Doug Heard, Mika Sutherland, Mark Williams.
Session chairs:	Jan Edmonds, Shane Mahoney, François Messier, Don Russell, Dale Seip, Don Thomas.

Preface

At the fourth North American Caribou Workshop in St. John's, Jim Davis suggested that the next Workshop address the issue of how ecological theory can be applied to practical caribou management problems. In addition to that theme, we also chose to highlight cooperative caribou management boards and the conservation and management of woodland caribou.

All of the papers on cooperative management boards stressed that boards must consider both local knowledge and information collected by scientists and they must attempt to blend native and bureaucratic approaches to decision making. A multicultural approach should expose, and therefore avoid, the unquestioned or unrecognized biasses which we all have:

> Cultural influences have set up the assumptions about the mind, the body, and the universe whithin which we begin; pose the questions we ask; influence the facts we seek; determine the interpretation we give those facts; and direct our reaction to these interpretations and conclusions. (Gunnar Myrdal *An American Dilemma* 1944).

Cooperative management boards should not only provide an opportunity for users to participate in the management of the resources that they rely on but also develop better management decisions.

To enlighten caribou researchers to the possibility that «cultural» influences also narrows our view of the world, we invited Gary Belovsky, Lee Eberhart, and Mitch Taylor, who's experience was primarily outside the area of caribou research, to apply their expertise in theoretical ecology to caribou management problems.

As elsewhere, there is a close association between caribou and people in the Northwest Territories. The workshop logo depicted that relationship and maintained our awareness of that fact throughout the workshop. We were happy to see that the public and interested groups from in and around Yellowknife took advantage of the opportunity to learn more about caribou biology and management. The entire second year class of the Renewable Resource Training Program from the Thebacha Campus of Arctic College in Fort Smith attended and both the Denendeh Conservation Board and the Beverly and Kaminuriak Caribou Management Board scheduled meetings in Yellowknife to correspond with this workshop.

These manuscripts were not subjected to peer review and were not edited to scientific content so that flashes of unbridled brilliance would not be excised by unimaginative and repressive editors.

Doug Heard and *Mark Williams.*

Insights for caribou/reindeer management using optimal foraging theory

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Abstract: Optimal foraging theory is useful to wildlife managers, because it helps explain the nutritional value of different habitats for wildlife species. Based upon nutritional value, the use of different habitats can be predicted, including how factors such as insect harassment, predation and migration might modify habitat selection. If habitat value and use can be understood, then changes in habitat availability which are of concern to wildlife managers can be assessed. The theory is used to address diet choice and habitat use of caribou/reindeer. Diet choice is examined in terms of lichen composition of the diet and is demonstrated to be a function of daily feeding time, food abundance and digestive capacity. The diet choice model is then used to assess the nutritional profitability of different habitats and which habitat should be preferred based upon nutritional profitability. Caribou/reindeer use of habitats is demonstrated to be easily modified by insect harassment and predation which change the nutritional profitability of habitats differentially. The same type of approach could be used to explain migratory behaviour; however, the needed parameter values are unavailable. The results of this analysis lead one to question some common conceptions about caribou/reindeer ecology.

Keywords: Caribou, reindeer, foraging theory, habitat choice, modelling, habitat preference

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Introduction

Modelling the foraging behaviour of herbivores has been attempted by several ecologists (Westoby, 1974; Owen-Smith and Novellie, 1982; Stenseth and Hansson, 1979; Ritchie, 1988; Schmitz, 1990; Belovsky, 1978, 1984a, b, 1986 a, b, submitted; Ball, 1990). In most cases, these models have met with a high degree of predictive success (Belovsky, submitted), but none have dealt with mammals that normally migrate or are allowed to migrate today (e.g., bison). Therefore, modelling the foraging behaviour of a species like caribou/reindeer *(Rangifer. tarandus)* that exhibits migratory behaviour in some populations might not be amenable to the same considerations that have been successfully applied to other species. In addition, the migratory behaviour of carbou/reindeer poses some interesting management considerations concerning why certain habitats are chosen within a given locale, why certain habitats are chosen seasonally, and how changing conditions (e.g., predator densities, human disturbance, etc.) might modify these choices.

I apply existing models of herbivore foraging that have proven successful for other species to the diet choices of caribou/reindeer employing data from the literature. With the potential value of these models established employing the available caribou/reindeer data, I proceed to ask questions about what habitats these herbivores should utilize seasonally based on feeding efficiency, insect harassment and predation employing other aspects of foraging theory (Stephens and Krebs, 1986). This analysis provides insights into how changing environmental conditions might affect caribou/reindeer populations through habitat use in ways which might be of concern to managers.

What is foraging theory and what is its use to managers?

Foraging theory emerged in the mid-1960's as an attempt to link animal food choices with population carrying capacity (MacArthur and Pianka, 1966; Emlen, 1966). While this field of investigation developed into one of the few areas of ecology where mathematical theory and empirical tests were in accord (Stephen and Krebs, 1986), its successes were more in the arena of animal behaviour, especially psychobiology, than population ecology. A few studies have carried foraging theory into the realm of population dynamics (Werner, 1977; Werner and Mittlebach, 1981; Belovsky, 1984a, 1986a) with success. Recently, the theory has been specifically applied to questions of wildlife management, i.e., winter supplemental feeding of white-tailed deer (Schmitz, 1990).

How pertinent is the theory to the detailed investigation of wildlife management problems?

The theory has been invoked in a number of models directed towards managing wildlife populations (e.g., Hobbs ans Swift, 1985; Hobbs and Hanley, 1990) based on predicting carrying capacity and/or habitat utilitzation. The potential use of such models appears to be high; however, some recent studies appear to have inappropriately applied the theory (Schmitz and Belovsky, submitted). One concern is that the detail required for wildlife management may be beyond the scope of current foraging theory. This arises from the inability of any study simultaneously to address generality, precision, and realism (Levins, 1967), as all studies are limited to attaining two of the three characteristics at any instant. Generality refers to the model's applicability to a wide range of species and conditions; realism refers to the model's ability to capture the specific details of a particular species and environment. Most foraging models seek generality and precision at the expense of realism.

The issue of generality vs. realism is of special concern to wildlife biologists and managers. Because foraging theory seeks generality at the expense of realism, it becomes very easy for individuals concerned with particular biological details to dismiss the theory. However, science seeks the general explanation of patterns rather than simply cataloguing specific details. Stephens and Krebs (1986) point out that foraging models by their general nature must simplify and treat many biological details in a perfunctory fashion; these are the same details that are the focus of a lifetime of research by other scientists (e.g., learning behaviour, digestive physiology, etc.).

Foraging models, however, may be of value to wildlife managers; it depends on the level of detail in the question being asked. If a manager is concerned with assessing the probability of survival of big game animals to a certain age or size based upon foraging conditions, then this question is far too detailed to be realistically addressed using foraging theory. If a manager is concerned with gross predictions of diet choice by a wildlife species in different habitats to assess the nutritional value of the habitats, or assess potential environmental changes on the species' nutritional ecology, then foraging theory has value.

Foraging theory, which is based upon concepts of natural selection and behavioral "plasticity", may provide wildlife managers with conceptual insights to design better management plans based upon the flexibility of individuals composing the wildlife population. Recently, Keppie (1990) criticized wildlife studies for their failure to address ecological concepts, so principles might be identified that would provide a broader application of information to different management situations. Keppie (1990) points out that we have a multitude of specific studies for wildlife species that are tied to particular locations, but their ability to provide insights for other sites and conditions is weak because the studies did not address conceptual issues that span all sites and conditions.

While foraging theory has been invoked by wildlife biologists working with caribou/reindeer (e.g., Kuropat and Bryant, 1980; White, 1983; Skogland, 1984), it has not been applied critically to assess the theory's predictive value. This is not unusual; the majority of studies that invoke foraging theory have failed to test it quantitatively for the species being examined (Stephens and Krebs,.1986; Belovsky, submitted). The only caribou/reindeer study that attempted to test a foraging model quantitatively was Skogland's (1984) study of reindeer in Norway. Unfortunately, a mathematically inconsistent foraging model (Stenseth and Hansson, 1979) was applied to the problem (Belovsky, 1984a). Additionally, serious problems in parameter estimation can be identified; it appears that food types may have been measured in a manner inappropriate to the modelling approach (i.e. food abundance), and digestibility values for lichen and non-lichen food types are not in accord with most literature values (see Table 3). Therefore, the apparently successful predictions of the model must be questioned.

Below I apply a foraging model to address whether caribou/reindeer choose food types consistent with the theory. Since the needed parameter values must be gleaned from the literature, and none were collected specifically to meet the requirements of the theory, some caution must be exercised in interpreting these results. Finally, the model is extended to examine habitat use patterns by caribou/reindeer.

The basic foraging model

Diet choice by mammalian herbivores has been predicted for a wide range of herbivore species and environments using the optimization technique called linear programming with more success than any other model yet applied (Belovsky, submitted). The validity of these models has been questioned (Hobbs, 1990; Hanly, 1980), but no better alternative has been presented and most of the criticisms are as questionable as the points raised against the foraging models (Belovsky, 1990).

Linear programming is an optimization technique that explicitly includes constraints (limits) to actions. The constraints define a combination of actions that are feasible, i.e., sets of actions that do not violate the constraints. Linear programming then employs various mathematical algorithms (e.g., Simplex) that identify the combination of actions which maximizes or minimizes some goal within these constraints (Intriligator, 1972). This methodology is based upon the assumption that constraints can be written as linear functions.

From previous studies of mammalian herbivores, four classes of constraints can be considered: digestive processing, feeding time, nutritional requirements, and food toxicity. Justification of these constraints and how they are constructed are discussed by Belovsky (1984a, 1986a). How these constraints will be applied to caribou/reindeer using data from the literature are discussed below.

To develop a foraging model for caribou/reindeer, one detailed data set (White and Trudell, 1980a, b; Trudell and White, 1981) will be employed extensively, because it provides more of the needed parameters than any single study and presents these for specific habitats. Diet choices will be examined for late July in two distincts habitats, high-centre polygons and lake margins, that caribou/reindeer must choose between at this time. The diet will be defined in terms of two food categories, lichens and non-lichens (e.g., shrubs, grasses, forbs, and sedges). These two habitats are of interest given the seasonal and daily movements of caribou between them (White and Trudell, 1980a, b; Trudell and White, 1981, White *et al.*, 1975; White, 1983), and the special interest in lichen consumption by caribou given its poor nutritional value (Klein, 1970).

Digestive processing of plant tissues is often considered to constrain the amount of plant food that an herbivore can ingest in some fixed period (e.g., day) (Westoby, 1974). This requires knowledge of the ability of digestive organs to hold food (capacity: mass/day) and the rate at which digesta passes through these organs (turnover: times filled/day). Capacity multiplied by the number of times this capacity can be filled provides a simple estimate of the animal's ability to process foods. This digestive processing ability is differentially utilized by the consumption of different foods that fill this capacity to varying extent (bulkiness: capacity filled/mass of food intake).

Digestive capacity might be defined either in terms of wet or dry mass. Hobbs (1990) argues that digestive processing ability should be measured in terms of dry, rather than wet, mass, and that bulkiness should be measured in terms of cell wall content (%/g-dry mass). However, using a digestive constraint based on dry mass in a linear programming model, Hobbs (1990) was unable to predict mammalian herbivore diets, as has been regularly found in other studies (Belovsky, 1990). There are physiological reasons and data to use dry matter and cell wall content (Hobbs, 1990; Belovsky, 1990), but there also are contrary physiological reasons and data to use wet mass (Belovsky, 1990). Therefore, choosing between these conflicting explanations for digestive capacity is not possible, and begs additional and redesigned physiological studies, but constraints based upon wet mass successfully predict mammalian herbivore diet choices in linear programming models (Belovsky, 1990).

The problem of defining the digestive capacity constraint based on dry vs. wet mass can be partially addressed using data for reindeer (Table 1). It can be demonstrated that daily food intake (g-dry/day/kg) is a significant negative function of food wet mass to dry mass, while cell wall content, measured as % fiber, is negatively correlated with intake, but not significantly. Therefore, wet mass appears to be a better basis for measuring the digestive constraint based upon this limited information, and was employed to construct the diet choice model presented here.

Table 2 presents the summary of data on caribou/reindeer that was used to construct a digestive constraint. Bulkiness (g-wet/g-dry) of the non-lichen foods in the two habitats differs, because the species composing those available in the lake margin tend to have a higher water content.

Feeding time seldom will encompass a complete 24 hr day, because animals are restricted in their feeding activity to time periods when digestive processing ability is not exceeded, thermal physiology is not limiting, and other activities are not being conducted (e.g., insect harassment, predator avoidance, mating, etc.). This feeding time is utilized differently in the acquisition of each of the foods (cropping time: min/g-dry). The parameter values for this constraint appear in Table 3.

For mammalian herbivores, digestive fill and thermal physiology seem to be most important in determining feeding time (Belovsky, 1986a). This may be the case for caribou/reindeer, as well. An important

Table 1. Daily food intake as a function of food bulk and cell wall contents using data from Syrjälä *et al.* 1983.

Parameter	Coefficient	t-value	P
Constant	27.19	8.23	0.004
Bulk	-2.35	-4.52	0.02
Cell wall content	-0.15	-2.1	0.13

Regression N=6, r=0.94, F=10.47, P<0.044

point is that thermal physiology may not limit activity via the animal being stressed to near lethal levels; rather activity may be limited by physiological changes relative to some set point chosen by the animal, and to times when activity may be least costly in terms of energy expended for thermoregulation (Belovsky, 1981, 1984b; Schmitz, in press). Winter feeding activity is often ascribed to heat loss limits (Gaare et al., 1975), but is summer activity limited by thermal physiology?

Caribou/reindeer may be able to tolerate environmental conditions that lead to heat gains to the same extent as African ungulates, but to do so they must "work" harder at thermoregulation (Yousef and Luick, 1975), and they do demonstrate heat stress (Ryg, 1975). While insect harassment clearly restricts feeding activity on warm and still days (White *et al.*, 1975; Helle and Aspi, 1983; Wright, 1980), these weather conditions also lead to greater thermal stress. Therefore, without better studies, these two factors, insect harassment and heat stress, cannot be separated in explaining reduced summer activity. This dilemma is further reinforced since caribou move towards the sea on warm, still days to escape insects (White *et al.*, 1975), but the coast will also provide thermally less stressful summer conditions, i.e., cooler and windier.

Cropping time (min/g-dry) should be a function of food abundance and distribution (Belovsky, 1986a), a prediction upheld for caribou/reindeer (Trudell and White, 1981; White and Trudell, 1980a; Skogland, 1980, 1984). However, Trudell and White (1981) argue that daily feeding time is limited by cropping rate, i.e., a constant intake of food that just satisfies nutritional requirements is sought, with the result that feeding time declines as food becomes more abundant. This can be explicitly tested using foraging theory and is the predicted outcome for the foraging goal called feeding time minimization (see below).

Nutritional requirements are the maintenance needs of an individual required to ensure survival. The maintenance requirements provide a set point against which discretionary additional intake by the forager can be compared. The additional intake can be allocated to growth, storage (i.e., fat) or reproduction. Three potential nutritional requirements are frequently listed for caribou/reindeer: energy, protein, and sodium.

Energy is the ultimate limiting factor in all ecological systems, and this is the best understood aspect of animal nutrition. The foraging model must include the individual's energy requirements to survive in the environment and how different foods satisfy this requirement (gross energy content x digestibili-

Table 2. Development of the digestive capacity constraint for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Rumen/reticulum contents (g-wet) = 11293 ln (mass in kg)-35703 N = 25, r = 0.96, P < 0.001	Staaland *et al.* 1979, Egorov 1965
Fraction of rumen/reticulum contents that is food = 0.29	White and Gau 1975
Turnover of rumen/reticulum in both habitats = 1.68 X's/day	White and Trudell 1980a, b
Bulk - lichen: 2.54 g-wet/g-dry	Staaland *et al.* 1986, Syrjälä *et al.* 1980, Valtonen 1980
non-lichen: high centred polygon: 1.66 g-wet/g-dry	Batzli *et al.* 1981, A. Rodgers unpublished
lake margin: 2.05 g-wet/g-dry	Batzli *et al.* 1981, A. Rodgers unpublished

Constraint: high centred polygon habitat 5980 g-wet/g-dry $\geq$ 2.54L + 1.66 NL
lake margin habitat 5980 g-wet/g-dry $\geq$ 2.54L + 2.05NL

Table 3. Development of the feeding time constraint for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Feeding time: high centred polygon – 305 min/day	White and Trudell 1980a, b
lake margin – 373 min/day	White and Trudell 1980a, b
Cropping time: lichen: 0.08 min/g-dry	White and Trudell 1980a, b, Trudell and White 1981
non-lichen: 0.15 min/g-dry	White and Trudell 1980a, b, Trudell and White 1981
Constraint: high centred polygon habitat 305 min/day $\geq 0.18L + 0.15\ NL$	
lake margin habitat 373 min/day $\geq 0.08L + 0.15NL$	

ty). The energy constraint values are presented in Table 4. This does not imply that energy is limiting to survival, since other nutrients might limit survival and adequate energy is acquired along with other nutrients.

Protein is often considered important to the nutrition of herbivores, because plant tissue is frequently low in protein, especially proteins composed of the essential amino acids required by animals. This is of special concern for caribou/reindeer, because of their habit of frequently consuming large quanitities of lichens that are low in protein (Klein, 1970). The protein constraint values are presented in Table 4. As with energy, protein may not be limiting survival, but adequate intake might be acquired along with other nutrients.

Sodium is often in low concentrations in plant tissue, especially in areas that have been glaciated and are located far from oceanic salt impaction (Botkin *et al.*, 1973; Belovsky and Jordan, 1981). Recent studies indicate that caribou/reindeer may experience and exhibit sodium deprivation in the summer months (Staaland *et al.*, 1983; Staaland and Jacobsen, 1983; Staaland *et al.*, 1980; Staaland *et al.*, 1981). The sodium constraint values are presented in Table 4. Again, sodium might not be limiting survival, but adequate amounts are acquired along with other nutrients.

Food toxicity from plant secondary compounds is often considered an important aspect of herbivore diet choice (Freeland and Janzen, 1974). Many plant secondary compounds (e.g., tannins) may reduce digestibility so their impact is incorporated in the nutritional constraints (Belovsky and Schmitz, 1991). However, plant secondary compounds that are potentially toxic to the herbivore must be explicitly built into the foraging model (Belovsky and Schmitz, 1991).

Lichens are known to contain many potentially toxic compounds (Rundel, 1978; Burkholder and Evans, 1945; Burkholder *et al.*, 1944). The importance of plant secondary compounds in caribou/reindeer foraging strategies has been argued (Kuropat and Bryant, 1980, 1983; Bryant and Kuropat, 1980). A constraint based on the ingestion of one of these compounds, pulvinic acid, is presented in Table 5. Pulvinic acid, a toxin peculiar to lichens, was employed because all of the necessary aspects of its actions on mammals (LD50 and concentration in plants) could be found in the literature (Rundell 1978).

Foraging goals are the outcome of foraging behaviour favoured by natural selection. This outcome could be determined either by the forager's variable behaviour ("plastic" response) or genetically fixed behaviour ("hard-wired" response). In the first case, selection would operate upon the flexibility in behavioral responses and learning ability of individuals, while in the latter case selection would operate directly upon an individual's foraging behaviour (e.g., a set of fixed diet choices). Most mammalian herbivores demonstrate a wide range of foraging behaviours ("plastic" response) and selection may operate on the ability to be flexible (Ritchie, 1990). In foraging theory, these foraging behaviours are often viewed to achieve two alternate goals: feeding time minimization and nutrient maximization (Belovsky, 1986a; Stephens and Krebs, 1986).

Feeding time minimization is the goal when the forager's fitness increases more with time spent in activities other than feeding (e.g., hiding from predators, mating, etc.). Because an individual must attain all of its nutritional requirements, this goal would have the forager attain these requirements in the least time spent foraging, so more time is available for other activities.

Table 4. Development of the nutritional requirements for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Energy:	
maintenance metabolism = 4646 kcal/day	Holleman *et al.* 1980, Young and McEwan 1975, McEwan and Whitehead 1970, Steen 1968
gross energy content:	
lichen = 4.36 kcal/g-dry	Holleman *et al.* 1979, McEwan and Whitehead 1970
non-lichen = 5 kcal/g-dry	McEwan and Whitehead 1970
dry matter digestibility:	
lichen = 46%	Russell and Martell 1984, Jacobsen and Skjenneberg 1975, Person *et al* 1975, 1980a, b, White *et al.* 1984, Thomas and Kroeger 1981, Thomas *et al.* 1984, Staaland *et al.* 1983, Luick 1972.
non-lichen = 54%	Person *et al.* 1975, 1980a, b, White and Trudell 1980b, White *et al.* 1975, Thomas and Kroeger 1981, Thomas *et al.* 1984, Staaland *et al.* 1983, Luick 1972, White *et al.* 1975.
Constraint: $4646 \text{ kcal/day} \le 2.01L + 2.70NL$	
Protein:	
Maintenance requirement = 115 g/day	Steen 1968, McEwan and Whitehead 1970, Holleman *et al.* 1980
Protein content:	
lichen = 2.8%	Person et al. 1980b, Wales *et al.* 1975, White *et al.* 1984, Pullianen 1971
non-lichen:	
high centred polygon = 14%	Scotter 1972, Staaland *et al.* 1983, Luick 1972
lake margin = 14.6%	Scotter 1972, Staaland *et al.* 1983, Luick 1972
Constraint: high centred polygon: $115 \text{ g/day} \le 0.028L + 0.14NL$ lake margin: $115 \text{ g/day} \le 0.028L + 0.146NL$	
Sodium:	
Maintenance requirement = 1.1 g/day	Staaland *et al.* 1981
Sodium content:	
lichen = 0.03%	Staaland *et al.* 1981, 1983, Staaland and Jacobsen, Luick 1972
non-lichen:	
high centred polygon = 0.05%	Staaland *et al.* 1981, 1983, Staaland and Jacobsen, Luick 1972
lake margin = 0.04%	Staaland *et al.* 1981, 1983, Staaland and Jacobsen, Luick 1972
Constraint: high centred polygon: $1.1 \text{ g/day} \le 0.0003L + 0.0005NL$ lake margin: $1.1 \text{ g/day} \le 0.0003L + 0.0004NL$	

Nutrient maximization is the goal when the forager's fitness increases more with the additional intake of some nutrient that limits survival and reproduction, than time spent in nonfeeding activities. The nutrient most frequently addressed in foraging theory is energy, but could be protein, sodium, etc., or even minimization of toxin intake.

Nutritient maximization is usually seen as the expected goal when the intake of nutrients determines reproduction and survival, so that population density would increase with greater food intake by individuals. However, feeding time minimization does not imply that food availability is not important to individual survival and reproduction, and population density. A feeding time-minimizer's fitness increases if more food is available, even though food intake per se is not limiting, because acquistion of nutritional requirements in less time makes more time available for other fitness-increasing activities. Therefore, to argue that food availability is only important to nutrient maximizers is incorrect.

The above observation means that clear distinctions between food limitation, predator limitation, etc., of populations is not easy to assess. For example, if predation is limiting an animal's fitness, then we might expect the animal to be a time minimizer, because it may be more exposed to predators while foraging and need to spend more time hiding from predators. The forager and its population would benefit, greater fitness, when food is more abundant, since nutritional requirements will be obtained in less time which means less time exposed to predators. If exposure to predators does not increase with foraging, then there would be no benefit provided by a time-minimizing goal and the forager would always be a nutrient maximizer, even when predators reduce survival and reproduction. This is even more apparent when we realize that these foraging goals are endpoints along a continuum.

The above distrinctions between fitness limits are important for caribou/reindeer. First, caribou/reindeer are known to have their survival and reproduction limited in some regions by nutrition (e.g., Adamczewski *et al.*, 1987, 1988; Leader-Williams, 1980, Skogland, 1985a, b; Roby, 1980). Other studies claim predation to be the principle limit to caribou populations, i.e., more food would not increase populations (Bergerud, 1980). From the above discussion, claims of predator limitation may not imply that food is unimportant to the caribou/reindeer population. This is why other investigators have argued that food availability and predation or insect harassment may be important at the same time (Reimers, 1980; Haber and Walters, 1980; Helle and Aspi, 1983). Therefore, assessing the importance of food to caribou/reindeer populations, even when predators are abundant, cannot be accomplished without careful analysis of caribou/reindeer feeding behaviour and their foraging environment.

The simulatenous importance of food and predation to populations has been most evident in studies using foraging theory applied to bluegill *(Lepomis macrochirus)* in the presence and absence of their predator, the largemouth bass *(Micropterus salmoides)* (Werner, 1985). These basic ecological studies have forced sportfishery managers and aquaculturists to reevaluate their assessment of food limitation versus predator limitation. The same problem must be addressed for caribou and the foraging model developed below may provide some insights.

Solving the foraging model

Using the constraint equations developed in Tables 2–5, a graphical representation of the linear programming foraging model can be developed (Fig. 1). The graphical portrayal illustrates how the different constraints restrict the caribou/reindeer's diet choices in the two environments to define a feasible set of diets: these are the diet combinations of lichens and non-lichens that satisfy the constraints. The toxin constraint for pulvinic acid in lichens was incorrect or not operating, since it is apparent that caribou/reindeer consume a diet containing more lichen than expected from the toxin constraint. Most likely, the caribou/reindeer are better at detoxifying the pulvinic acid than rodents upon which the LD50 was based (Rundell, 1978). These results indicate the need for better measures of toxicity before the importance of secondary compounds can be quantitatively assessed via foraging models (sensu Belovsky and Schmitz, 1991).

The linear programming model can be used to solve for the two potential goals: feeding time minimization and nutrient maximization (Intriligator, 1972). The predicted diets are crude, since the model parameters were not measured to satisfy the foraging model's criteria (e.g., cropping rates were not measured instantaneously, g-dry/min for individual food types, but by food intake measured using fistulated animals, g-dry/longer time period, which can include behaviours other than foraging and can combine the intake of both food types). Nonetheless, certain possibilities can be identified.

1) If energy is the only limiting nutrient requirement, then a time-minimizing diet would consist of 100% lichens in both habitats (Point 1 in Fig. 1A, B),

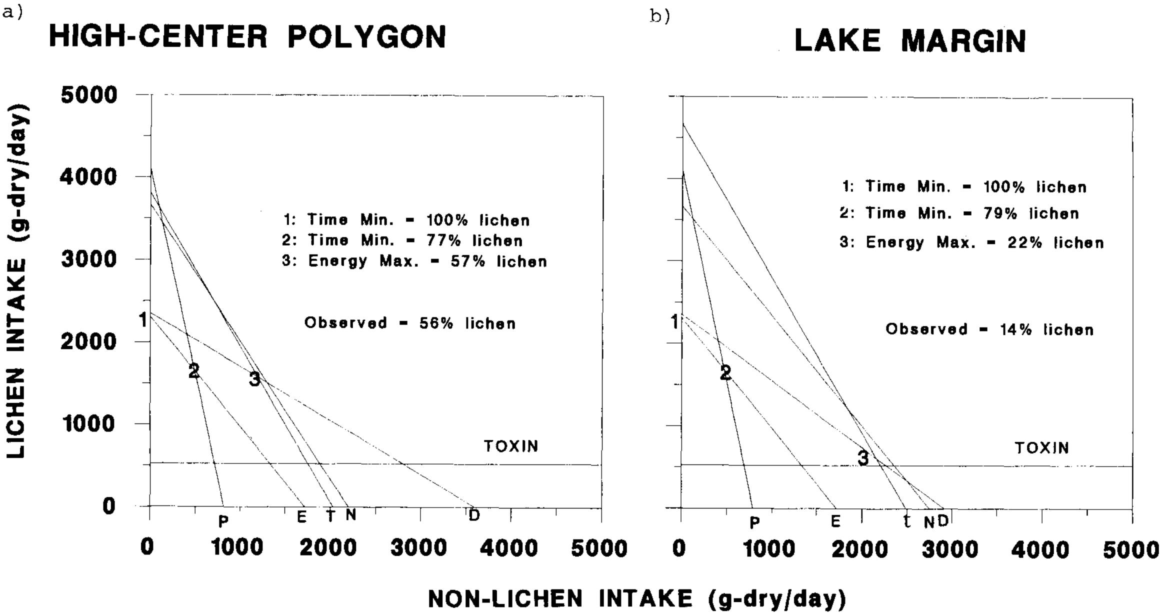

Fig. 1. The graphical representation of the linear programming diet model for caribou/reindeer is presented for the high-centre polygon habitat (a) and the lake margin habitat (b). The letters along the x-axis identify the constraints (Tables 1-4) (P is protein, E is energy, T is feeding time, N is sodium, D is digestive processing), and the flat line parallel to the x-axis is labelled TOXIN for secondary compounds. Each graph presents the observed diet and 3 solutions to the model (ignoring the toxin constraint, see text): 1) the time-minimized diet based only on an energy requirement; 2) the time-minimized diet based on energy and protein requirements; 3) the energy-maximized diet, ignoring the sodium requirement (see text).

but the observed diets are 56% in the high-centre polygon and 14% in the lake margin habitats. Therefore, either there are other nutrient requirements not satisfied along with energy requirements, or the caribou/reindeer are not time minimizers.

2) If energy and protein are limiting nutrients, then a time-minimizing diet would consist of 77–79% lichens in the two habitats (Point 2 in Fig. 1A, B). Again this is very different from the observed diets, indicating that the caribou/reindeer do not act as time minimizers or other nutrient constraints are operating.

3) The energy-maximizing diet consists of 57% lichens in the high-centre polygon and 22% lichens in the lake margin habitats (Point 3 in Fig. 1A, B). Both of these values are very close to those observed. Without detailed information on the diet samples which are not provided in the studies (White and Trudell, 1980a), a statistical comparison cannot be made. Nevertheless, it appears that these animals could be energy maximizers. But what about the maximization of other nutrients? It cannot be protein because a diet composed of 100% non-lichens would be predicted by protein maximization. This indicates that caribou/reindeer do not appear to be maximizing protein intake in anticipation of consumption of low-protein lichens during winter. Thus, the idea that protein limits caribou populations (Klein, 1970) is brought into question. This leaves maximization of sodium intake as the only other possibility.

4) Using the sodium constraint, we find that the caribou/reindeer in either habitat cannot attain their minimum requirement measured in summer (Staaland *et al.*, 1981). The energymaximizing diet in this case also maximizes sodium intake, so either energy or sodium intake could be the goal. However, if sodium is in such short supply, how do the caribou/reindeer acquire adequate amounts of sodium in the summer? Possibly, this is achieved by the consumption of small amounts of aquatic vegetation that is high in sodium content (Staaland and Jacobsen, 1983), as found for moose *(Alces alces)* (Belovsky, 1978).

It would be useful to determine the reliability of the model's predictions, given the confidence intervals of the model's parameters (sensitivity analysis). This can be done using Monte Carlo simulations (Belovsky, 1984b, submitted). However, most of the confidence limits for the parameters are not reported. Therefore, a sensitivity analysis could not be attempted.

An additional evaluation of the model can be performed by making qualitative predictions about how diet composition will change with food depletion (White and Trudell, 1980a, b). White and Trudell (1980a, b) tethered caribou/reindeer in a small area for 3 days (314 m^2) and the abundance of non-lichens was depleted more than lichens over this period. If a caribou/reindeer is a nutrient-maximizer (energy or sodium), it should: a) consume less lichens as feeding time increases, and b) consume more lichens as the more nutritious, in terms of energy, non-lichens decrease in abundance. The first prediction is affirmed by comparing diets in the two habitats. The second prediction also is affirmed. If the caribou/reindeer were time minimizers, the diet (77–79% lichens) would not have changed.

From the model, we can reach several conclusions, assuming that the parameter values are adequate to build a foraging model. First, the caribou/reindeer appear to be nutrient-maximizers. Second, the lake margin habitat is superior (1.13 times) to the high-centre polygon habitat from an energy intake perspective, and more so based on dry matter intake (1.33 times). Third, the major difference between the two habitats is due to differences in feeding time. Fourth, because the caribou/reindeer at these sites are nutrient-maximizers, this suggests that they would have greater survival and reproduction if food were more abundant, assuming that the observed feeding times reflect the maximum values for these habitats (see below).

The above points illustrate the importance of the feeding time constraint to developing a foraging model. Trudell and White (1981) originally argued that the difference in feeding time for the two habitats is due to the animal's maintaining a set nutritional intake which results in less time spent feeding when food is more abundant. Their argument is equivalent to a time-minimizing goal. Because the observed goal is energy maximization, we should seek explanations for the observed feeding time differences elswhere (e.g., insect harassment, predators, thermal environment, etc.). Furthermore, it is very difficult to attribute feeding time differences to differences in food abundance, when the measures of different food abundances are based upon different seasons and habitats (Trudell and White, 1981). This means that many other factors that affect feeding time will be changing concurrently with food abundance.

Additional support for the foraging model is provided by solving it for caribou/reindeer at other sites where their diet and daily feeding time are known (see Fig. 2). This is done assuming that all model parameters presented in Tables 2–4 are the same for these other sites, except for feeding time. The observed diets for these 6 additional sites are predicted very well ($r = 0.98$, Fig. 2), which illustrates the robustness of the model. The importance of feeding time is also reaffirmed, since it alone is varied in the diet model; feeding time in itself can explain the proportion of the diet composed of lichen very well ($r = -0.96$, $N = P \leq 0.01$), but not as well as the model. An interesting pattern emerges in Fig. 2. All the predicted diets contain more lichens than observed, this might arise if the toxins in lichens (Rundell, 1978) lead to reduced ingestion.

Habitat choice, predation and insect harassment

Foraging theory applications developed experimentally with fish (reviewed in Werner, 1985; Werner and Mittlebach, 1981; Werner and Gilliam, 1984; Gilliam and Fraser, 1987) can be used to address habitat use by caribou/reindeer. In the absence of natural enemies, a forager, whether an energy maximizer or time minimizer, will have its fitness determined by its energy intake rate (energy/time).

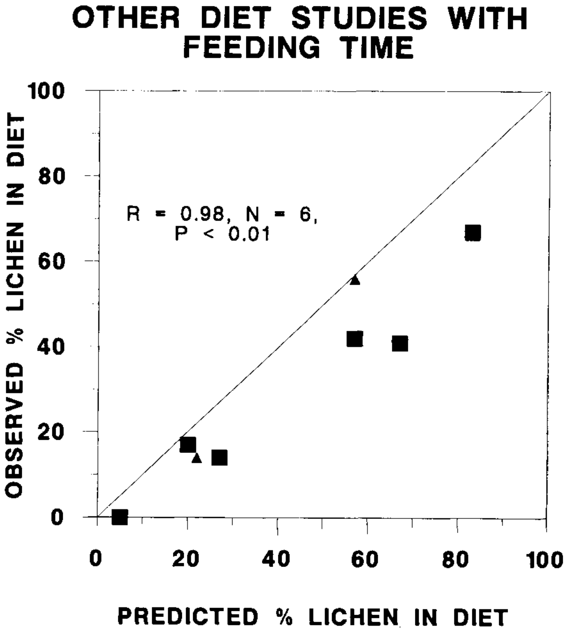

Fig. 2. The comparison of the predicted and observed proportion of the caribou/reindeer diet composed of lichens for 6 studies (squares: Wright, 1980; Skogland, 1984; Martell *et al.,* 1985, White *et al.*, 1975) is presented. The studies used to develop the linear programming diet model are also presented (triangles: White and Trudell, 1980 a, b).

With the greatest energy intake rate, a time-minimizer will satisfy its energy requirements in the least time, while an energy-maximizer will acquire the greatest energy intake in available feeding time. In this case, foragers, when presented with a variety of habitats, should choose to use the habitat that provides the greatest fitness. However, if natural enemies have an appreciable influence on an individual's fitness, then habitat selection based on energy intake rate can be modified, but energy intake rate will always be important.

The above conclusions are based upon the assumption that the habitat is neither depleted during the period of observation by the individual or by other individuals using the habitat during the same period. However, as the food becomes depleted, the individuals will distribute themselves according to the Ideal Free Distribution (Fretwell and Lucas, 1970; Fretwell, 1972). In the Ideal Free Distribution, individuals move or distribute themselves between habitats to maximize their fitness. Therefore, the second-best habitat in terms of fitness will be used only after a certain depletion of the best habitat or a certain accumulation of individuals within the best habitat. The outcome is that the best habitat will contain more individuals or more time will be spent in it, and all habitats utilized will be equally depleted, i.e., provide equal fitness.

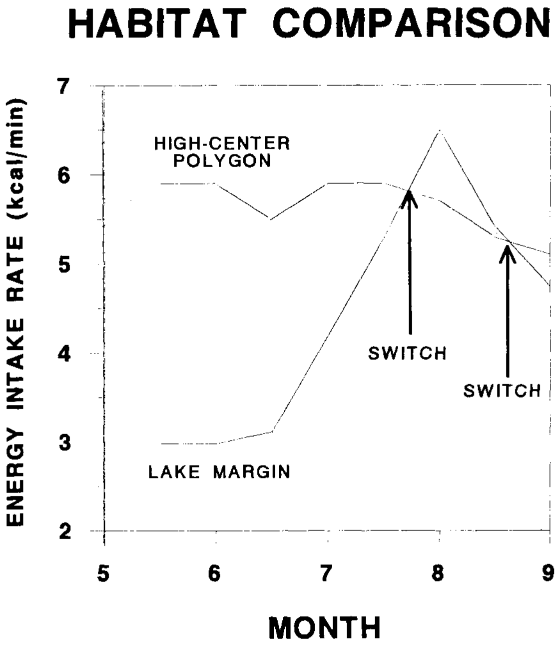

Fig. 3. The seasonal change in energy intake rate for caribou/reindeer in two habitats is presented. The optimum switching between habitats based upon energy intake rate is depicted. The relationship is adapted from White's (1983) representation of dry matter intake, and the linear programming diet model's conversion of dry matter intake into energy intake per minute.

Assuming that natural enemies do not appreciably influence fitness, we can make some predictions about shifts in habitat use over the summer for caribou/reindeer, using White's (1983) seasonal comparison of habitats based upon food intake. Because daily food intake (g-dry) overestimates differences between the lake margin and high-centre polygon habitats (see above), daily food intake was converted into daily energy intake. To control for differences in daily foraging time, so the nutritional value of the two habitats can be compared, the energy intake (kcal/day) is divided by daily feeding time (min/day) to compute a rate of energy intake (kcal/min). The habitats are compared in Fig. 3 based on the rate of energy intake. The high-centre polygon would be used in May, then the lake margin would be used in mid-July, and then the high-centre polygon would be used again starting in late-August. At any one time, if a habitat cannot accommodate all individuals or is depleted, the other habitat would then be used. Energy intake rate declines because cropping rates (g-dry/min) decline, which reduces food intake and/or changes the diet so more of the less nutritious food types are ingested.

As predicted above, caribou in late-July preferentially use the lake margins (proportion of animal-hours spent in the habit relative to the proportion of area) (White and Trudell, 1980a, b). This preference is not absolute (only one habitat used), since the caribou also use the high-centre polygons, and this use occurs before the food in the lake margins is depleted. Therefore, caribou appear to utilize the high-centre polygons more frequently than expected, given energy intake rates. What other explanations might be invoked to explain this greater than expected use of the high-centre polygon habitat? Two potential causes could be insect harassment and predation.

Insect harassment reduces a caribou/reindeer's daily feeding time (White *et al.*, 1975; Helle and Aspi, 1983; Wright, 1980). White *et al.* (1975) examine reduced feeding time as a function of the intensity of insect harassment, and the habitats where insects are most abundant. This study indicates: a) insect harassment is greater in the lake margins than the high-centre b) insect harassment increases as air temperature rises and wind speed declines; c) at moderate levels of harassment, feeding time declines by 27%

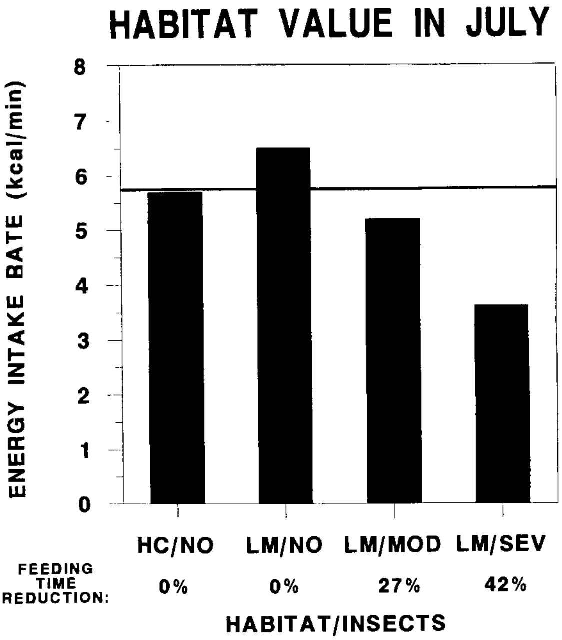

Fig. 4. The comparison between the energy intake rates in July for caribou/reindeer in two habitats, where one habitat (LM: lake margin) has higher biting insect abundances. The lake margin energy intake rate must fall below the horizontal line before the other habitat (HC: high-centre polygon) will be used. This occurs at moderate and worse levels of insect harassment in the lake margin habitat.

and at high levels of harassment the decline is 42%. The observed feeding times used in the foraging model cannot be attributed to insect harassment. First, the observed feeding times are not influenced by insect harassment, since White and Trudell (1980a, b) claim that the measures of feeding time were made on days of minimum harassment. Second, if harassment were important, we would expect less feeding time in the lake margin, not more as observed.

Using the above observations for reduced feeding time in the lake margin habitat, the foraging model can be solved using the reduced feeding time. At moderate and high levels of harassment, the caribou should prefer the high-centre polygon habitat, since energy intake rate (kcal/min) there becomes greater than in the lake margin habitat (Fig. 3). Therefore, insect harassment can influence habitat choice by modifying nutritional return. This may be the reason why the caribou do not demonstrate an absolute preference for the lake margin during summer.

Predation could also operate in a similar manner to insect harassment by reducing an individual's feeding time due to the need to spend time being vigilant for predators (Lima *et al.*, 1985). Reimers (1980) makes this claim for wolves and human hunters on caribou/reindeer. Roby (1980) compared caribou/reindeer feeding time at two sites, one with wolves and the other without wolves. He found *greater* feeding time in the presence of wolves; however, this study compared two very different sites (Alaska vs. Greenland). To investigate these assertions, there must be much greater control over site differences that also might influence feeding time. Therefore, these data are not definitive, nor are there adequate data for other ungulates inhabiting open habitats in the presence and absence of predators.

In addition to decreased feeding time due to increased vigilance, predation can cause additional changes in foraging behaviour. If *healthy* individuals are killed (non-compensatory predation sensu Errington, 1956), predators reduce an individual's expected fitness through increased mortality. This effect of predation can be easily incorporated into foraging theory using linear programming and has been empirically tested using fish (Gilliam and Fraser, 1987; Gilliam, 1990). When presented with two habitats, as is the case investigated here, a set of simple predictions can be made based upon the ratio of mortality rate to energy intake rate:

1) if the forager can move between both habitats quickly (close proximity), then

    a) the forager will only use the habitat with the highest energy intake rate, if it also has the lowest mortality rate (minimum ratio of mortality to energy intake rate);

    b) if 1a is not the case and the forager seeks a set nutritional intake, the forager will feed in both habitats; this is accomplished by preferentially utilizing the habitat with the lowest mortality to energy intake ratio, but spending sufficient time in the other habitat to attain the set nutritional intake (non-feeding time will be spent in the habitat with the lower mortality, i.e., refuge);

2) if the forager cannot move easily between both habitats (not close proximity), then

    a) it will spend all of its time in the habitat with the lowest ratio of mortality to rate of energy intake, if it can attain its set nutritional intake in this habitat;

    b) if the set nutritional intake cannot be attained in the above habitat, but can be obtained in the other habitat, the animal will ignore the ratio of mortality rate to energy intake rate (i.e., select the habitat based solely on energy intake rate).

We know from the diet model that the caribou/reindeer do not forage to attain a set energy intake, because they are energy maximizers; therefore, case 1b and 2b can be discounted. This distinction is important, because the only condition left is selecting one habitat that minimizes the ratio of mortality rate to energy intake rate (cases 1a, 2a). This observation does not preclude the use of one of these habitats (or others) as refuges when the caribou are not feeding, which is observed (White and Trudell, 1980a, b). How much greater would the mortality rate due to predation have to be for a caribou/reindeer to shift its use of the lake margin to the high-centre polygon?

Wolves would have to be 14% more effective as predators in the lake margins than in the high-centre polygon to make the ratio of mortality rate to energy intake rate equal for the two habitats. This would eliminate any preference for the two habitats and illustrates how small a difference in predation is needed to cause habitat shifts. If the caribou avoided the habitat that provides a greater energy intake rate because of predation, the potential for food limitation of their population would be enhanced. Perhaps the killing of prey by predators is far less important to limiting prey populations than the ability of predators to enhance food limitation for their prey. Interestingly, Bergerud (1980) lists the caribou used in the foraging model (Western Arctic herd) as being limited by wolf predation.

Is there any evidence that wolves have differential predatory impacts on caribou in the two habitats? Miller (1982) argues that caribou are cautious when in areas of dense willow and brush, fearing ambush by a predator. Crisler (1956) and Kelsall (1968) indicate that caribou are more vulnerable to ambush by wolves, than to pursuit in the open. Shrubs are much more abundant in the high-centre polygon habitat, perhaps making wolf predation more effective there. Therefore, caribou may be more vulnerable in the high-centre polygon habitat.

The potentially greater predation risk in the high-centre polygon habitat may be the reason for the lower feeding time observed there, if the caribou spend more time being vigilant. If the caribou could increase their foraging time in the high-centre polygon in the absence of wolves, they *might* have a greater energy intake rate there than in the lake margin habitat and might preferentially use the polygon habitat. The lake margin habitat *is* preferentially used by the caribou. Caribou might prefer the lake margin because of its greater energy intake rate in the presence or absence of predators, but they might use the high-centre polygon habitat less than the lake margin, because of predation. Without better data (mortality rates, and energy intake rates in the absence and presence of predation), this type of scenario cannot be evaluated, but will have important consequences for caribou management.

Migratory behaviour of caribou/reindeer is often attributed to the individuals' search for better food resources (Kuropat and Bryant, 1980; Whitten and Cameron, 1980; Skogland, 1980; Tyler and Oeritsland, 1989). This can be addressed using the same approaches developed above, where the energy intake rates for habitats that are far apart are compared after incorporating the amortized energy costs of migration. If the costs include reduced feeding time, this can be incorporated by discounting the energy gains obtained in each habitat after migration. Tyler and Oeritsland (1989) found that, during migration, daily feeding time is reduced by 21%. If the costs include increased mortality due to predators or exhaustion, this can be incorporated as was done above by using the ratio of mortality rate to energy intake rate. If the migratory benefit is in reproduction above that provided by better nutrition, this can be considered, but reproduction becomes the currency and energy intake will have to be converted into reproductive units. An attempt to perform such an analysis for migrating African ungulates was provided by Fryxell *et al.* (1988).

The data necessary to evaluate migratory behaviour are unavailable, but if they were, one could evaluate the impacts of reduced migration on caribou populations. This is an important management question given that migration routes are being disrupted and distinct habitats that are seasonally used are disappearing.

Conclusions

The utility of foraging theory to address questions about caribou/reindeer ecology is apparent from the above discussion. I do not wish to imply that the analyses that I presented above are definitive, because the available data were not collected to meet the parameter criteria of foraging models. These criteria include measurements made at the same site where the feeding studies were conducted, and over the time frame required for the constraints (e.g., instantaneous cropping rates on a single food type, see above). However, the results do illustrate the potential that the theory provides in understanding caribou/reindeer ecology. These ecological questions are not only of scientific interest, but they have important implications for management decisions.

I used the linear programming diet choice model to investigate interactions (trade-offs) between digestive physiology, feeding time/food abundance, nutritional requirements and toxins, and the diet choice model was built into habitat selection models to investigate interactions between food intake, insect harassment, and predation. The results raise more questions than possibilities eliminated. For example, the foraging model only examined two food categories: lichens and non-lichens. Can the foraging model explain the variable intake of the plants composing the non-lichen category: grasses, sedges, forbs and shrubs? For example, the habitat choice model demonstrated how predator avoidance might reduce feeding time. Is feeding time reduced in the presence of predators or do other factors such as thermal physiology restrict feeding time more? These are but a few of the questions emerging.

Based upon foraging theory some basic explanations of caribou/reindeer ecology must be questioned. These include: feeding time being limited by food abundance (e.g., Trudell and White, 1981), summer food abundance and quality not being important (e.g., Reimers, 1980), and wolf predation, rather than food, limiting caribou populations (e.g., Bergerud, 1980). Rather than seeking a single explanation, the interactions between factors should be investigated (e.g., food and predation sensu Haber and Walters, 1980). Clearly, food limitation is not necessarily the simple observation of starving animals or overgrazed range, as sometimes claimed (Bergerud, 1978, 1980), and a better understanding of nutritional ecology is needed before other factors (e.g., predation) can be designated the most important limit to caribou/reindeer populations.

To make these types of comparisons, we need better data on wildlife. This will involve the manipulation and control of environmental conditions. When factors are not controlled, or at least measured for comparison (e.g., interplay between digestive physiology, thermoregulation, insect harassment and predatory risk in determining daily feeding time), it becomes very difficult to ascribe causality. I was able to formulate the diet choice model for caribou/reindeer because of a wide range of data already available, and even more importantly, the innovative *experimental* methods employed by Trudell and White (White and Trudell, 1980a, b; Trudell and White, 1981). These experimental methods are a first step toward eventually being able to distinguish among alternative explanations for feeding time, habitat usage, and a host of other caribou/reindeer attributes critical to effective management.

While ecologists such as myself are thrilled by the ability to predict quantitatively the biological details that represent species, populations and communities, this type of detailed understanding is just as critical for good management. Mautz (1978) argues that our ability to manage is limited by the weakest link in our knowledge. While this is in part true, I would also argue that we need to ask whether more detailed observations must be accumulated, or greater understanding might be achieved by developing and testing concepts; this is the dilemma of generality vs. realism.

Conceptual understanding might enable a manager to answer a priori how habitat changes, restricted migration, increased predator densities, etc., might affect the nutritional status of caribou/reindeer, and subsequently, their population densities. Even with detailed knowledge of species' biology, a manager might not be able to address these questions without a conceptual framework. Foraging theory provides this type of general conceptual framework with which fairly robust and valuable predictions can be made using the minimum of detailed information. The elegance of these general and minimal models in comparison to more complex approaches (e.g., simulation models) is that the underlying explanations are more easily identified, and can then be experimentally tested, so the model can be verified and validated (Jeffers, 1982).

Acknowledgements

I wish to thank J. B. Slade and D. Skelly for reading and commenting on this manuscript, and O. J. Schmitz for pointing out to me the potential application of foraging theory to caribou/reindeer given the available literature.

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Printed from manuscript after editorial review.

Proceedings of the Fifth North American Caribou Workshop

Models of ungulate population dynamics

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Abstract: A useful theory for analyzing ungulate population dynamics is available in the form of equations based on the work of A. J. Lotka. Because the Leslie matrix model yields identical results and is widely known, it is convenient to label the resulting equations as the "Lotka-Leslie" model. The approach is useful for assessing population trends and attempting to predict the outcomes of various management actions. A broad list of applications to large mammals, and two examples specific to caribou are presented with a simple spreadsheet approach to calculations.

Keywords: Modelling, ungulates, Leslie matrix model, Lotka-Leslie model

Rangifer, Special Issue No. 7: 24—29

Introduction

The material presented here was prepared for a workshop session having the theme "Incorporating ecological theory into research design". The major issue in modelling ungulate population dynamics is the lack of suitable field data. We never have enough data and frequently delude ourselves that in any defensible way. This lack of good data leads me to be very pessimistic about many aspects of what seems to pass as ecological theory these days. A few years ago some of these concerns were suggested in a note about testing hypotheses (Eberhardt 1988a).

The Lotka-Leslie model

There is a body of theory that fits the overall theme of incorporating theory into practice very well indeed, and that has been neglected in practice. This is the theory developed by A. J. Lotka about 80 years ago, which underlies modern studies of demography. Another expression of the same general approach was presented by P. H. Leslie in two papers in the 1940's (Leslie 1946, 1948). Calling the underlying theory the "Lotka-Leslie model" provides a useful reminder of the equivalence of the two approaches.

To justify such a label, one needs to review a little background. Lotka's approach was via continuous mathematics, no doubt inspired by the need to accommodate the human habit of reproducing at any season of the year. His principal result was thus expressed as an integral equation. On the other hand, Leslie used matrix algebra, and thus considered events at discrete points in time, so that the reproductive elements in this model are often described as averages or approximations.

Inasmuch as caribou (and many other wildlife species) give birth only in a short time interval each year, it is possible to avoid many of the complications of the usual demographic analyses. L. C. Cole (1954) developed the necessary equations for such a discrete approach. It turns out the principal equation is the same as that widely used as an approximation to Lotka's equation, which cannot be solved directly in its integral form. Hence, for species like caribou, there is a simple and direct approach in discrete mathematics.

Cole thus provided a very useful formulation and his paper should get more attention in textbooks than usually is the case. Actually, it does get cited quite a bit for another aspect. Probably it is worthwhile to digress here, and mention that issue, in view of the suggestion that we should consider "the demographic parameters that are most influential in terms of caribou numbers". That can be done very simply - adult female survival is the most important such feature. This is readily demonstrated, and there likely are now a dozen papers in the recent literature addressing that point. I have had occasion to stress it in two papers (Eberhardt and Siniff 1977; Eberhardt *et al.* 1982), both of which deal with species (marine mammals and feral horses) having reproductive and survival rates somewhat similar to those of caribou.

Feral horses, however, start giving birth much earlier in life than marine mammals, and thus illustrate an important secondary feature of population dynamics, i.e., appreciably higher population growth rates are possible when habitat conditions permit first births at age 2 rather than at age 3. Cole was intrigued by this feature and described it for the range of species from bacteria to large mammals. On such a scale, the age of first reproduction does indeed have an impressive effect on population growth rates, and academic types thus often tend to stress that aspect. Hence we need to remember that caribou are not insects, and that much of the population dynamics material found in textbooks is derived from data on insects.

Returning to the main theme here, the Leslie matrix approach starts with a listing (a vector) of the number of individuals in discrete age classes and projects that listing to produce a new such listing one or more units of time in the future, adding in gains from reproduction and losses due to mortality. Recalling that we are dealing with a species that gives birth in a short time period each year, it is most convenient to suppose that the youngest individual in a given population is almost one year of age in the initial listing (age vector). The next observation of the population is made one year later, so that the survivors of the initial population are a year older, and the youngest is again just under one year old. Consequently, the reproductive elements in the matrix which projects the population forward are the product of a birth rate and survival for the first year of life.

In contrast, Lotka's formulation treats the population just *after* births take place, and thus is formulated somewhat differently, leading to a good deal of confusion in the ecological literature. Fortunately, anyone who can make simple calculations with any of the many "spreadsheet" programs now available for personal computers can readily dispose of this confusion by simply calculating the two approaches. However, one further feature of the underlying theory needs to be mentioned first.

This is the "stable age distribution" which is produced if one projects a population having virtually any initial age structure sufficiently far forward in time. The underlying theory shows that not only will the population age structure attain a given form, but that the population will change at a constant rate as that "stable" age structure is attained. Unfortunately, details of the time required to approach the stable state and the nature of that approach depend on the initial age structure and are usually expressed via the calculus of complex domains. Practically speaking, however, one can avoid most of these complications by doing some spreadsheet calculations to evaluate the effects of various realistic initial age structures. The theory does, however, give us an equation "characterizing" the Leslie matrix approach (the "characteristic polynomial"), that can be compared with Lotka's equations.

For the present, we need only note that the stable age distribution can easily be computed by a simple equation derived by Lotka. Once this has been done in a spreadsheet, it is then a simple matter to project this age distribution forward in time, using the same reproductive and survival rates as used in Lotka's equations, but proceeding by the rules underlying Leslie's matrix approach. Doing this in a spreadsheet yields exactly the same population growth rate as that predicted by Leslie's matrix approach, providing one retains fractional "animals" in the calculations. Rounding off to the nearest whole individual, as happens in reality, provides a useful reminder not to use many decimal places in expressing a population growth rate.

Using the Lotka-Leslie model

Thus far, we have considered the elements of a theory of population mathematics established by demographers in some 80 years of research and application. (Books by Keyfitz (1968) and Pollard (1973) describe details, history, and applications to human populations; Eberhardt (1985) described some applications to wildlife populations). Some immediate questions are, "What good is it to wildlife managers?", and "Why isn't it used more in wildlife management?"

I suspect that the answer to the second question lies in part in my initial one-word statement of what matters most, i.e., data. A reasonably short answer can be provided for the first question by considering the kinds of observations collected in wildlife studies and what is done with them. Mostly, one sees a lot of ratios calculated and discussed in general terms and relative to similar ratiaos from other places and times, such as age ratios, sex ratios, young-adult ratios, and the like. The other common element is some measure of population trend, along with harvest data. If the trend changes somehow, then we try to interpret it in terms of the auxiliary information provided by the various ratios. Too frequently, the results of such interpretations are not very convincing nor very helpful in deciding what to do next.

In my view, the advantage of a theory of population dynamics is that it provides a framework within which the available data can be analyzed and interpreted. Whether the analysis is very helpful in management seems to me mostly a matter of the completeness and quality of the information available for a given population. The essential ingredients are survival and reproductive rates, from which one can estimate an expected rate of increase or decrease, subject to the requirement that the stable age distribution holds. In my experience this is not a very important restriction, as can be demonstrated by experimenting with changes in age structure in a spreadsheet model of the kind described previously here. However, this optimistic view does not extend to estimating survival rates from single samples of age structure data. Such estimates are quite sensitive to fluctuations in age structure.

Ideally, one would be able to confirm the findings of an analysis based on censuses or an index of some kind. In practice, it often turns out that some essential rate is not available, such as first-year survival. It is then possible to use the model to estimate the missing item of information.

How can the Lotka-Leslie model be used in real-life management? One obvious way is just as a means to understanding what's going on in a population. Trend data provide a sufficient basis for management only as long as nothing changes, and no change in management action is contemplated. Sex and age ratios usually defy interpretation unless one also has the results of a Lotka-Leslie type of analysis, in which case the ratios are likely not to be of much interest, anyhow. Table 1 lists some applications of this kind of analysis in practice, but is limited to cases in which I have had some direct experience.

Some caribou examples

The next question is "how does one obtain the necessary data?" Reproductive rates are not too difficult to obtain. The difficult part, of course, is obtaining survival data. One way is via radiotelemetry, but this approach is very expensive, even for species with a more limited range than caribou. The alternative is to use age structure data. The usual approach is to estimate survival from a single age structure sample. If the population is changing, one has to correct for that fact, using an independent estimate of the rate of change. An example is the data for the George River herd given by Messier *et al.* (1988: Table 5). Their approach involves fitting a smoothed frequency curve, and yields a steadily declining survival rate, which seems somewhat doubtful, on the basis of experience with other large mammals. A problem is that the age frequency curve should decline throughout, but does not in this case. An alternative is to use a subset of age classes in which survival is likely to be nearly constant (say, age 3 to age 12), and the Chapman-Robson "segment" method (Robson and Chapman 1961) to the original data, and correct for changing population size by multi-

Table 1. Some applications of the Lotka-Leslie model.

Species	Application	Reference
Whitetailed deer	Planning and assessing impact of antlerless harvests	Eberhardt (1969)
Feral horses	Assessing population growth rates. Devising management strategies	Eberhardt et al. (1982) On-going
Bowhead whales	Evaluating role of delayed maturity and impact of Eskimo harvests	Breiwick et al. (1984)
Hawaiian monk seals	Searching for causes of persisting low levels after decline	On-going
Fur seals	Appraising population decline and continuing low levels	Eberhardt (1981, 1990)
Grizzly bears	Assessing decline and future prospects (Yellowstone N. Park)	Knight and Eberhardt (1985)
Elk	Evaluating population trends	McCorquodale et al. (1988)
Caribou	Further studies of decline in Nelchina herd	Eberhardt and Pitcher (submitted)
Sea otters	Impact of Exxon Valdez oil spill	On-going
Pacific walrus	Impacts of harvests on population	On-going

plying by λ (cf. Eberhardt 1988b). This gives an unadjusted rate of 0.837 (S.E. = 0.016), which becomes 0.837 (1.11) = 0.929 on correction. Some allowance for senescence is needed to construct a survivorship curve, and might be obtained by fitting the curves described in Eberhardt (1985).

A second example is available in data presented by Thomas and Barry (1990a). These authors also smoothed age data by fitting a quadratic, using pooled age data from 6 successive years (1981–1986). Trend data were not available, and it was indicated that "a review of the survey data suggests little change has occurred since 1967". It may then be appropriate to pool the age data for the 6 years. This was done by summing the data of Table 3 of Thomas and Barry (1990a) along diagonals, i.e. entries of the same age-class; the data of Table 3 were arranged by cohorts. Using the first 10 age-classes reported and the Chapman-Robson segment method as above, gives s = 0.852 (S.E. = 0.012). An alternative is to calculate survival rates for each year. In this example, the average of the yearly survival rates is virtually that of the pooled data. Because a constant population size is assumed, no correction for population growth is needed (i.e., we assume $\lambda = 1.0$).

Adult survival for the Beverly herd is thus appreciably less than for the George River herd, as might be expected. An immediate question is whether these rates can somehow be checked from the data at hand. Because population trend data were used to correct the apparent survival rates calculated from the age data (explicitly for the George River herd and implicitly for the Beverly herd) it does not, at first glance, seem sensible to use the Lotka-Leslie model to also calculate a rate of increase. However, it can be argued that such a calculation does provide some evidence as to internal consistency. This is because the age structure depends only on survivorship, and not on reproductive rates. That is, the stable age structure is calculated as (cf. Eberhardt 1985: 998):

$$c_x = B\,\lambda^{-x}\,lx \qquad [1]$$

where $B = 1/\sum \lambda^{-x} l_x$. Reproductive rates do, of course, influence population growth, but do so by determining λ from solution of the "Euler equation":

$$1 = \sum_{w}^{a} \lambda^{-x} l_x\, mx \qquad [2]$$

where l_x = survival to age x, and m_x = female births per female of age x, age of first reproduction is denoted by a, and w represents the last age considered.

Calculating λ from the observed survival and reproductive rates thus can provide some evidence of the internal consistency of the data. Rather than attempting to fit a curve to represent senescence, one can use an approximation as suggested by Eberhardt (1985: 1007), but some extra terms are added here to take into account lower reproductive rates in the first few age classes. Messier *et al.* (1988: Table 5) give m_x values of 0.06 for age 2, 0.35 for age 3 and 0.40 for ages older than 3. If we truncate at age 12 (to compensate for senescence), calculations of λ can be carried out in a spreadsheet model. Messier *et al.* (1988: Table 5) give survival to age 1 as 0.71, and 0.99 for age 1 to age 2. Inasmuch as it appears unlikely that survival in a younger age class would be so much higher than that of adults, the rate calculated above is used here from age 1 onwards, so that $l_x = 0.5\,(0.929^{x-1})$. One can then calculate values of eq. [1] in a spread-

Table 2. Entries for a spreadsheet model for eq. [1], based on data from Thomas and Barry (1990a, 1990b).

Age	m_x	l_x	$\lambda^{-x} l_x\, m_x$	$\lambda^{-x} l_x$	c_x	s_x
0		1		1	0.2242	0.63
1		0.63		0.63038	0.14133	0.8
2	0.06	0.504	0.03028	0.50461	0.11313	0.852
3	0.36	0.42941	0.15487	0.43018	0.09645	0.852
4	0.43	0.36586	0.1577	0.36673	0.08222	0.852
5	0.43	0.31171	0.13444	0.31265	0.0701	0.852
6	0.43	0.26558	0.11461	0.26653	0.05976	0.852
7	0.43	0.22627	0.09771	0.22722	0.05094	0.852
8	0.43	0.19278	0.0833	0.19371	0.04343	0.852
9	0.43	0.16425	0.07101	0.16514	0.03702	0.852
10	0.43	0.13994	0.06054	0.14078	0.03156	0.852
11	0.43	0.11923	0.05161	0.12002	0.02691	0.852
12	0.43	0.10158	0.044	0.10232	0.02294	0

sheet, changing λ until the equation balances. For the George River herd, using the l_x and m_x values given above, the result is $\lambda = 1.096$, reasonably close to the observed 11% population growth rate.

Thomas and Barry (1990a: Table 2) gave first year survival of 0.50 and second year survival of 0.80. Using these values with the adult survival of 0.852 and the m_x values of Thomas and Barry (1990b) yields $\lambda = 0.964$, appreciably below the value (1.0) needed for a constant population size. Inasmuch as the first and second year survival rates were "developed by assuming 50% survival to 1 year and 20% mortality from age 1 to 2 years". (Thomas and Barry 1990a: 178), it seems reasonable to adjust these rates to see what values are needed to achieve constant population size ($\lambda = 1.0$). Setting $l_1 = 0.63$ yields the desired result. Entries for a spreadsheet calculation to achieve this result appear in Table 2. The entries in the 4th column ($\lambda^{-x} l_x m_x$) are summed, and λ is varied by trial and error until that sum is virtually unity. The c_x entries are calculated as in eq. [1], which uses the values in the 5th column of the table ($\lambda^{-x} l_x$). Values of s_x in the final column are calculated as $s_x = l_{x+1}/l_x$, and serve as a check.

Discussion

I believe that estimates based on a single age structure sample need to be regarded as being useful mainly for exploratory studies. To meet management goals, better estimates should be developed. A prospect that is worth pursuing is to use age structure samples in successive years, weighted by a measure of population trend. One can then estimate survival rates as the ratio of the abundance of an age class in one year to its abundance in a previous year. To minimize chance fluctuations a series of age classes need to be combined. An effort along these lines for fur seals was described in Eberhardt (1990), and a similar attempt for caribou was developed by Eberhardt and Pitcher (submitted).

A final point needs to be considered. The Lotka equations can serve as an analytical device, combining reproductive and survival rates to estimate a rate of increase. These same rates can then be used to project a population forwards in time. However, most practical problems are more complex and need some modifications, and likely a little modelling. One thus uses these tools as a starting place. Perhaps one of the most difficult issues in going further, is "what to do about density dependence?" Often one cannot neglect that issue, but the subject is certainly not well understood as yet. My own inclination at present is to suppose that density dependence operates initially (and perhaps mainly) on first-year survival, and to represent this by a "generalized logistic" curve, as used, for example, by Breiwick *et al.* (1984). Skogland (1990: Fig. 7) presents data suggesting a decrease in first-year survival with increasing density from which one might approximate the needed curves.

Acknowledgements

This research was supported in part by the Environmental Research Dvision of the Office of Health and Environmental Research of the U.S. Department of Energy under contract DE-AC06-76-RLO1830.

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Printed from manuscript after editorial review.

Proceedings of the Fifth North American Caribou Workshop.

Limiting factors in caribou population ecology.

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Abstract: Caribou and wild reindeer populations fluctuate over time. On this fact there is general agreement. Factors responsible for population limitation and subsequent declines have been examined within the framework of animal population theory. There is, however, little agreement when factors limiting specific populations are generalized to *Rangifer* populations over broad geographic regions. Comparative examinations of wild *Rangifer* populations worldwide discloses that factors that have regulated those populations are highly variable between populations, apparently as a reflection of the differences in environmental variables unique to each population. Examples exist of populations where major regulating factors have been climatic extremes, predation, hunting mortality, food limitation, insects, parasites, disease, interspecific competition, and human developmental impacts or combinations of these factors. This diversity of limiting factors affecting caribou and wild reindeer populations is a reflection of the ecologial complexity of the species, a concept that has often been ignored in past efforts to reach management decisions by extrapolation from the limited localized knowledge available on the species.

Keywords: Population dynamics, hunting, predation, food, climatic influence, parasites, diseases, interspecific competition.

Rangifer, Special Issue No. 7: 30—35

Caribou and wild reindeer populations fluctuate over time in response to a variety of population regulating factors. No single factor is universally responsible for these fluctuations. Each herd has a unique set of environmental constraints with which it interacts. In most cases mulitple factors are at play, although at any one time a single factor may dominate in its regulatory effect on the herd. Because of the migratory nature of large herds, their ecosystem relationships are more complex than is the case for nonmigratory wildlife.

Hunting pressure

Hunting has accounted for the limitation of growth and reduction of *Rangifer* populations worldwide. In North America excessive hunting pressure has been implicated in reductions of the Nelchina (Bos 1975), Western Arctic (Davis *et al.* 1980), and Fortymile (Davis *et al.* 1978) herds in Alaska and the Bathurst, Beverly, and Kaminuriak herds in Canada (Calef 1981). Today, in Alaska regulated hunting pressure is a primary factor controlling the Adak, Nelchina, and Delta herds. Hunting accounted for the near extinction of the Svalbard reindeer (Wollebaek 1926), and hunting has been the primary regulating factor of wild reindeer herds in Norway (Reimers *et al.* 1980) and the large Taimyr herd of the Soviet Union (Syroechkovski 1986).

Predation

Predators, primarily wolves, have been associated with population limitation of the Delta Herd (Davis *et al.* 1983) in Alaska and small herds of woodland caribou in Canada (Bergerud 1983). While predation has been invoked as the primary limiting factor on other herds, such as the Nelchina in Alaska (Bergerud and Ballard 1988) and the large caribou herds in northern Canada (Bergerud 1983), opposing viewpoints cite contrary evidence (VanBallenberghe 1985; LeHénaff and Luttich 1988). Predators clearly interact in an additive or compensatory way with other regulatory factors such as hunting mortality, climatic extremes, and food limitation in their degree of influence on caribou populations.

Food limitation

Constraints on food availability associated with population control of *Rangifer* populations have been most frequently documented in situations where other controlling mechanisms, such as predation, hunting pressure or dispersal were absent or constrained. Island introductions have experienced classic overgrazing and associated population «crashes» or declines (Scheffer 1951; Klein 1968; Leader-Williams 1988). Insular populations in the Arctic have also fluctuated in relation to food abundance and availiability; the New Siberian Islands (Kischinskii 1971) and Coats Island in Hudson Bay (Adamczewski *et al.* 1986), being of particular note. West Greenland caribou (Thing 1984) and Norwegian wild reindeer herds (Skogland 1985) have also fluctuated in response to density-food relationships.

In northern North America, where large predator populations have remained intact, food limitation of caribou herds has been poorly documented. The George River Herd in Quebec-/Labrador (LeHénaff and Luttich 1988) and the Southern Alaska Peninsula Herd (Pitcher *et al.* 1990) appear to be exceptions where declining body condition, reduced calf production, and increased mortality appear to be tied to constraints on seasonal forage quantity and quality.

Climatic extremes

Climatic extremes may account for increased mortality of caribou, either directly as in the case of loss of newborn calves to hypothermia during windy or wet conditions (Kelsall 1953) or indirectly as when extreme snow depths or icing conditions limited access to forage (Klein 1968; Miller *et al.* 1982). Climatic extremes have been more frequently documented as limiting caribou populations in the High Arctic and on islands than has been the case among the larger continental herds (Parker *et al.* 1975; Kischinskii 1971; Adamczewski *et al.* 1986).

Extinction of the endemic subspecies of caribou in East Greenland at the turn of the last century is believed to have been brought about by a series of winters with extreme snow accumulation (Vibe 1967). The synchrony of population fluctuations of most large caribou herds across North America during the past two decades appears to be most parsimoniously explained on the basis of continent-wide trends in weather patterns. There are, however, inadequate weather records for the regions involved to test this hypothesis.

Insects and parasites

The introduction of the warble fly and nasal bot fly to West Greenland with a shipment of domestic reindeer in 1952 resulted in apparent decreases in body condition and accentuated population lows among the caribou that previously had been free of these parasitic insects Clausen *et al.* 1980). In Svalbard, the absence of insect harassment and parasitic insects is believed to contribute to the population welfare of the endemic subspecies of reindeer (Reimers 1980). Extreme insect harassment and associated parasitism during and unusually warm summer is believed responsible for heavy mortality of calves during the subsequent winter among the Western Arctic Herd (Davis *et al.* 1980).

Caribou have much lower tolerance for infestation by the brain worm than deer that are the principal host species (Dauphiné 1975). It has therefore been speculated that the southern limits of caribou in North America are controlled by the northern distribution of deer (Bergerud 1983).

Disease

Disease has not been documented as the primary cause of population limitation among wild *Rangifer*, although it has been a contributing mortality factor in a few situations under conditions of high density and apparent food limitation. Colibacillosis has accounted for heavy loss of calves during summer among caribou in West Greenland (Clausen *et al.* 1980) and brucellosis increased substantially among the Western Arctic Herd in Alaska (Neiland *et al.* 1968) and the Taimyr Herd in Siberia (Syroechkovski 1986) under conditions of high density with concurrent reduced reproductive success.

Interspecific competition

Throughout much of the range of distribution of wild *Rangifer* muskoxen are the only other ungulate species present. Seasonal patterns of habitat use by the two species result in limited overlap in diet (Thomas and Edmonds 1984; Klein 1986), although under extreme winter conditions, when forage availability is limited by snow cover, direct competition may occur (Vibe 1967; Klein and Staaland 1984).

Grazing by domestic sheep in eastern Iceland has, over several centuries, altered plant composition, reduced plant biomass, and accelerated erosion in areas occupied by feral reindeer, with comcommitant reduction in the «carrying capacity» of the area for the reindeer, however, little direct competition for forage between reindeer and sheep appears to exist at present (Thorisson 1983).

Domestic reindeer and wild reindeer or caribou have a long history of direct competition for forage resources wherever they have occurred together (Klein 1980b). In the Soviet Union official management policy, until the late 1970's, encouraged the elimination of wild reindeer to allow for expansion of reindeer husbandry (Andreev 1975). During the 1980's it was recognized that management for wild reindeer could be far more productive in many areas of the USSR than reindeer herding, and policy was changed accordingly (Syroechkovski 1986).

Human development activities

The effects of human development activities on caribou and wild reindeer population dynamics have been the subject of widespread debate (Klein 1971, 1980a; Bergerud *et al.* 1984; Skogland 1986), often fueled by polarized support from development interests on the one hand and environmental advocates on the other. Behavioral responses of caribou to disturbances, including avoidance and range abandonment, have been documented in association with oil field development and development of transportation corridors, including roads, railroads, pipelines, and icebreaker traffic in rivers (Parovshchikov 1965; Klein and Kuzyakin 1982; Skogland 1986). Population responses to human development activities have not been as well documented, perhaps in some cases because of the lack of background information on the populations prior to development, a long lag time in population responses, and because of the difficulty in establishing cause and effect relationships for such an ecologically complex species. In Norway, construction of a highway and railroad transportation corridor resulted in obstruction of a traditional migration route for wild reindeer with associated overgrazing on the restricted available range, followed by a precipitous population decline (Skogland 1986). A similar population decline of wild reindeer as a result of railroad construction in northern European Russia has been reported (Parovshchikov 1965). Mountain caribou in the northern Rocky Mountains of the United States and adjacent Canada have suffered deterioration of habitat quality through logging of old growth forests and associated road and highway construction with corresponding population declines (Bloomfield 1979).

Unjustified assumptions and untested hypotheses

1) *Ecosystem relationships in the Arctic and Subarctic are simple:*

   Caribou belie this assumption. In contrast to other deer species living at lower latitudes, caribou show more plasticity of diet and habitat use throughout their distribution, and through migration they bridge ecosystems with their associated and unique predator, insect, and forage relationships.

2) *Nature tends toward stability:*

   At high latitudes, climatic extremes with interannual variations result in wide fluctuations in plant productivity and availability as forage, as well as having direct effects on survival of young, predator-prey interactions, levels of insect harassment, and energetic costs of locomotion and thermoregulation. Consequently, wide fluctuations in numbers of caribou is common as is also true of many other northern herbivores, such as lemmings, hares, and ptarmigan.

3) *Caribou populations cycle:*

   Caribou populations fluctuate widely over long periods of time and the possibility that caribou populations cycle with a periodicity of 65 or more years has been proposed (Meldgaard 1986). Unfortunately, estimates of population numbers of specific herds are reliable only during recent decades, therefore no adequate data sets exist upon which to test this hypothesis. To be cyclic, fluctuations in numbers must have a common periodicity.

4) *Population dynamics are influenced by exhange of caribou between herds:*
It has been hypothesized that when caribou populations increase to very high numbers large segments of these herds may «spill over» to join adjacent herds that may be at low levels and unable to «escape» from «predator pits»(Haber and Walters 1980). This «seeding» of small herds by large herds has been proposed as the mechanism that allows small herds to escape predator pits. Although cited by some authors (Kelsall 1968; Skoog 1968) as a possible explanation for initial caribou herd increase there is no documentation of exchanges of more than a few animals between herds. The increased frequency of use of radio collars to track caribou movements in recent decades should have provided evidence for large scale transfer of animals between herds if it had occured.

5) *Migratory caribou do not require lichens:*
This assumption is based on experimental feeding trials in which caribou were able to subsist quite well in the absence of lichens (Bergerud 1974), and observations that some populations of caribou and reindeer in the High Arctic and on islands have existed with virtually no available lichens (Thomas and Edmonds 1983). Thus, while it is true that high arctic populations at very low density, island populations under strong maritime climatic influence, and individual caribou and reindeer do not require lichens, the large migratory herds of the northern portions of North America and Eurasia are dependent upon lichens as the major winter forage resource that sustains their high population levels (Kelsall 1968; Andreev 1975; Holleman *et al.* 1979).

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Printed from manuscript after editorial review.

Detection of density-dependent effects on caribou numbers from a series of census data

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Abstract: The main objective of this paper is to review and discuss the applicability of statistical procedures for the detection of density dependence based on a series of annual or multi-annual censuses. Regression models for which the statistic value under the null hypothesis of density independence is set *a priori* (slope = 0 or 1), generate spurious indications of density dependence. These tests are inappropriate because low sample sizes, high variance, and sampling error consistently bias the slope when applied to a finite number of population estimates. Two distribution-free tests are reviewed for which the rejection region for the hypothesis of density independence is derived intrinsically from the data through a computer-assisted permutation process. The "randomization test" gives the best results as the presence of a pronounced trend in the sequence of population estimates does not affect test results. The other non-parametric test, the "permutation test", gives reliable results only if the population fluctuates around a long-term equilibrium density. Both procedures are applied to three sets of data (Pukaskwa herd, Avalon herd, and a hypothetical example) that represent quite divergent population trajectories over time.

Keywords: density dependence, census, randomization test, permutation test

Rangifer, Special Issue No. 7: 36–45

Introduction

Population studies of ungulates generally aim at identifying causes of population fluctuations, and density-dependent effects that lead to population regulation (Messier 1991a, b). The first objective requires the investigation of processes that quantifiably influence the population rate-of-increase, hence revealing their *limiting effect.* The second objective is more specific; it addresses density dependence of dominant population processes, such as food competition, predation, parasitism, and dispersal, to assess their *regulatory effect* on animal numbers (Fowler 1987; Messier 1989; Sinclair 1989). Density dependence may be revealed by analysis of changes in sources of mortality with population density (Sauer and Boyce 1983; Messier and Crête 1984, 1985; Skogland 1985, 1986; Freeland and Choquenot 1990). Alternatively, density dependence can be assessed at the population level using a series of census data (Vickery and Nudds 1984; Gaston and Lawton 1987; Pollard *et al.* 1987; Reddingius and den Boer 1989).

The population dynamics of caribou or reindeer *(Rangifer tarandus)* has been reviewed by many authors in recent years (Bergerud 1980, 1983; Leader-Williams 1980; Skogland 1985, 1986, 1990; Messier *et al.* 1988). Food exploitation, predation, and winter snow accumulation have been identified as primary limiting factors, although most authors stressed that the respective impacts of these agents on population growth likely differ according to caribou densities, presence of alternate prey, geographic region, and environmental factors (e.g., Van Ballenberghe 1985; Bergerud and Ballard 1988). However, the density relationships of dominant causes of mortality, primarily those involving biotic interactions, are still poorly documented (Messier *et al.* 1988). This lack of information continues to restrict our capacity to empirically understand the demography of caribou in North America, particularly the mechanisms involved in the regulation of caribou numbers.

The principal objective of this paper is to review and discuss the applicability of statistical methods for the detection of density dependence based on a series of annual or multi-annual censuses. Such analyses would be warranted when the density relationship of individual causes of mortality cannot be assessed due to limited information. Yet, the detection of overall density dependence would imply that one or a number of mortality agents reduce the population rate-of-increase at elevated densities, and *vice versa*. Mechanisms of population regulation are exhibited only when density dependence actually operates, not during periods of unlimited growth. Therefore, such tests may suggest the most appropriate time period to initiate a demographic study aimed at revealing feedback mechanisms in caribou population dynamics.

Tests of density dependence

The hypotheses

An animal population is said to be density independent if its growth rate is independent of the density of the population itself. Let N_t be the size of an animal population at a specific time in the annual cycle. A simple model of density independence is:

$$X_{t+1} = r + X_t + \epsilon_t \qquad [1]$$

where $X_t = \ln(N_t)$ $(t = 1, 2, ..., n)$, ϵ_t is an independent normal random variable with mean zero and variance σ^2, and r denotes a "drift" factor. A population governed by [1] follows a random walk through time with and average drift of r; there is no tendency for the population to return to a long-term equilibrium value.

An animal population is said to be density dependent if its growth rate is correlated with its size. The correlation must be negative to create population stabilization. A model of density dependence frequently cited in the literature takes the following form:

$$X_{t+1} = r + \beta X_t + \epsilon_t \qquad [2]$$

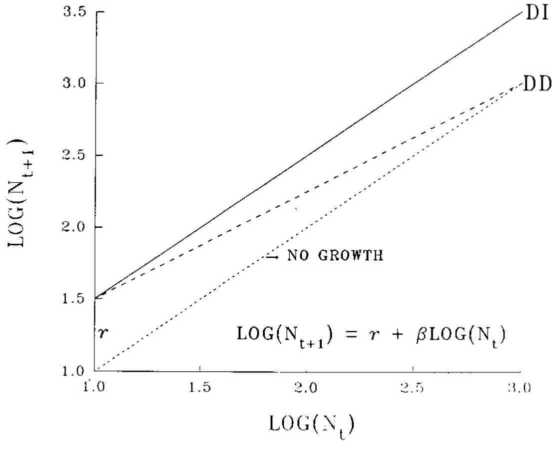

Figure 1. Test of density dependence proposed by Morris (1959, 1963), when applied to a series of censuses (N_t). It is hypothesised that $\beta = 1$ for a density independent (DI) population, and $\beta < 1$ for a density dependent (DD) population.

where β is a constant reflecting the degree of density dependence, and r, X_t, and ϵ_t conform to model [1]. Here, the population growth rate depends upon X_t when β #1. If $\beta = 1$, then model 2 converges to model 1. A population governed by [2], when $\beta < 1$, will tend to fluctuate around an expected value of $e^{r/(1-\beta)}$ (Fig. 1), which can be taken as the ecological carrying capacity (KCC, Macnab 1985). The variable r represents the population rate-of-increase assuming no density dependent effects, or $r_{\max}$ as defined by Caughley (1977: 53).

Models [1] and [2] essentially form the null and the alternative hypothesis to test for the presence of density dependence at the population level. Specifically, we are asking the following question: does the sum of negative feedback mechanisms affecting population growth outweigh the sum of the positive feedback mechansisms, thus creating population regulation (Berryman *et al.* 1987; Berryman 1991)?

Regression models

Regression analysis has been used by many authors to analyse population data (review in Itô 1972, Slade 1977). A first approach, proposed by Morris (1959, 1963), consisted of regressing $\ln(N_{t+1})$ on $\ln(N_t)$ for a series of annual censuses (Fig. 1). Density-independent populations should generate a slope (β) of one, and a y-intercept equal to r (the exponential rate-of-increase). Density dependence should be indicated by $\beta < 1$. Here, β is estimated by b, the slope of the regression line computed by standard least squares procedure (Sokal and Rohlf 1981: 468). Maelzer (1970), St. Amant (1970), and Itô (1972) noted four important weaknesses to this approach: (1) a problem of autocorrelation because each estimate of population size (except the first and the last ones) is used successively as x- and y-value; (2) the test is largely unsuitable for populations with large, stochastic fluctuations in numbers; (3) a density-dependent process frequently generates a curvilinear relationship on a log-log graph because of an accelerating impact at high densities, hence producing a relationship not appropriately described by a linear regression model; and (4) a population with a low intrinsic rate-of-increase, but with potentially wide displacements in densities through time (like caribou), will always be associated with a b-value close to unity. The major weakness of this approach, however, is the assumption that b is an unbiased estimator of β, and should equal 1 for a density-independent population (i.e., the null hypothesis). Computer simulations showed that such an assumption was in fact incorrect for finite sample sizes

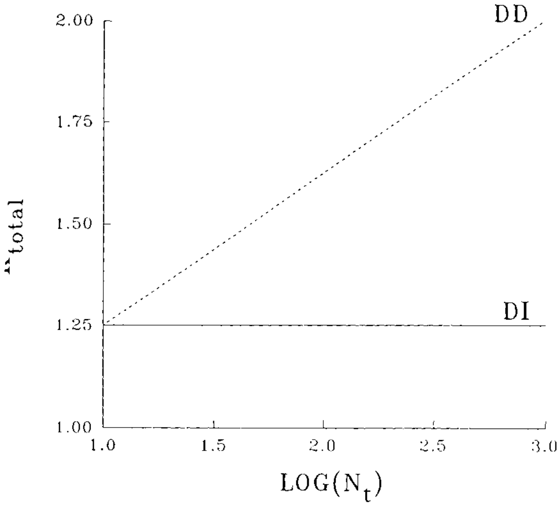

Figure 2. Test of density dependence proposed by Varley and Gradwell (1960), when applied to estimates of annual total mortality rates (k_{total}) versus log population size (N_t). Density independence (DI) should be associated with a slope of 0, whereas density dependence (DD) should be indicated by a slope greater than 0.

(Maelzer 1970; St. Amant 1970; Slade 1977). Non-regulated populations had a mean slope significantly less than 1, and the departure was greater for low sample sizes and variable data. Therefore, the test proposed by Morris often generates spurious indications of population regulation (Bulmer 1975; Slade 1977).

Varley and Gradwell (1960) presented another method for analysing serial census data which was expanded later by Krebs (1970), Watson (1970), Podoler and Rogers (1975), and Manly (1977). This method consists of expressing each source of mortality (frequently called "submortality") as the difference of $\log_{10}$ of population size before and after the submortality has acted. Each submortality, expressed here in *k*-values for a number of years, can then be plotted against log population size before its action to assess the degree of density dependence (Podoler and Rogers 1975). For age-structured populations, the analysis can be restricted to a given age class (Sinclair 1973; Clutton-Brock *et al.* 1987; Albon *et al.* 1987) or to animals of all ages (Clutton-Brock *et al.* 1985). However, a problem arises when the study animal has a complex life cycle. In such cases it is often impossible to sequence mortality agents through time because they may act simultaneously (a notable difference compared to many invertebrate species; Varley *et al.* 1973). Nonetheless, total mortality (k_{total}) from t to $t+1$ can be plottet against $\log(N_t)$ to reveal overall density dependence (Fig. 2; Itô 1972). Note that a regression expressing the rate of population growth against log population size is mathematically equivalent to a regression involving k_{total}, assuming that the loss of breeding potential is treated as a submortality (Kuno 1971; Clutton-Brock *et al.* 1985; Messier 1991a).

There is a serious empirical difficulty in applying the approach of Varley and Gradwell. The authors assumed that a density independent population should be indicated by a slope of zero when k_{total} values are plotted against log population size. Like the model of Morris described above, the slope is biased by data that contain low sample sizes and high variance (Itô 1972), thus providing erroneous evidence for density dependence. The fact that one cannot derive the *b*-value for the null hypothesis greatly hampers statistical testing for density dependence using key factor analysis.

Other regression statistics have been used to determine density dependence. These include (1) the slope of the principal axis, (2) the slope of the standard (reduced) major axis, (3) a comparison of the slope of a double regression [$\ln(N_{t+1})$ on $\ln(N_t)$, and $\ln(N_t)$ on $\ln(N_{t+1})$], and (4) the coefficient of first order serial correlation (see Varley and Gradwell 1963; Varley *et al.* 1973; Bulmer 1975; Slade 1977). However, recent Monte Carlo simulations have demonstrated that these statistics remain largely inappropriate to reveal density dependence (Slade 1977; Vickery and Nudds 1984; Pollard *et al.* 1987; Reddingius and den Boer 1989).

Non-parametric models

Pollard *et al.* (1987) suggested a simple, distribution-free approach for the detection of density dependence based on a series of annual censuses. The method uses the correlation coefficient, or the slope of the regression line, between the observed rate of population growth and population size (Fig. 3). A distinct feature of the proposed test is that the correlation coefficient under H_0 (i.e., model 1) is derived intrinsically from the data by a randomization process.

The rationale of the randomization test of Pollard *et al.* (1987) is rather simple. Let X_t (t = 1, 2, ..., n) be $\ln N_t$) for a series of annual censuses. If model 1 applies, $(X_2 - X_1)$, $(X_3 - X_2)$, ..., $(X_n - X_{n-1})$ are random fluctuations that sequentially displace the population size from X_1 to X_n. Writing $d_t = (X_{t+1} - X_t)$ (t = 1, 2, ..., n-1), the observed displacement of X_1 to X_n is due to a particular ordering of random d_t va-

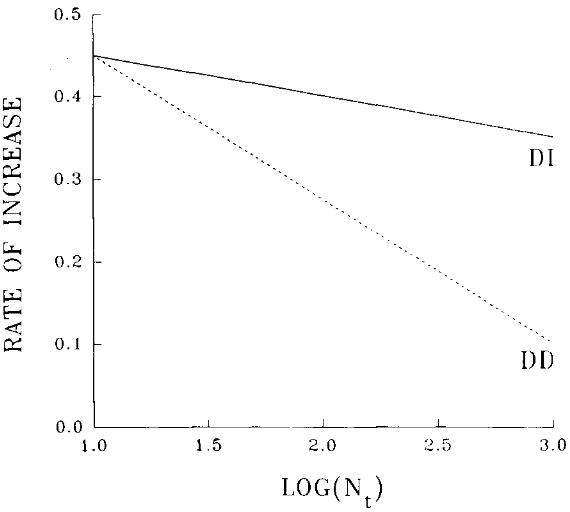

Figure 3. Illustration of the randomization test proposed by Pollard *et al.* (1987) where the annual exponential rate-of-increase is plotted against log population size (N_t). Density dependence (DD) should be indicated by a slope signifincantly lower than the slope associated with a density independent (DI) process. The density distribution of slopes under the hypothesis of density independence is derived from random permutations of the annual estimates of the population rate-of-increase.

lues. For a density independent population, d_t values could have occurred in a different order, generating a different, but equally likely, sequence of X_t values. Now we can run a large number of random permutations of d_t values to assess the correlation coefficient between d_t and X_t, symbolized here by r_{dx}. In essence, we are constructing the statistical distribution of r_{dx} under H_0, which we then use to assess to departure of the r_{dx} value computed from the original data set. If less than 5% of the r_{dx} values calculated from a randomization process are smaller than or equal to the computed r_{dx} from the original sequences of d_x, then reject the null hypothesis at 5% level of significance. In such cases, one concludes that the present survey data show evidence of density dependence.

It is important to realise that the test designed by Pollard *et al.* (1987) can be used as an alternative to a key factor analysis (Varley and Gradwell 1960) to reveal density dependence. Consider the following tautological equation:

$$k_{total,t} = r_{max} - d_t \qquad [3]$$

Clearly, k_{total} is simply the difference between the maximum rate of population growth under no ecological constraints, minus the realised growth rate for that year. The reader should notice that any loss of breeding potential is part of the total mortality in equation [3]. Thus, k_{total} and d_t are related by a constant (r_{max}), with no statistical effect on the regression analysis involving either d_t or k_{total} on X_t (Kuno 1971; Royama 1977). Monte Carlo simulations performed by the present author have indeed shown that the application of the randomization test on k_{total} values is mathematically equivalent to a test based on d_t values, with the notable exception that the slopes of the two regression lines have opposite signs (unpubl.).

Reddingius and den Boer (1989) have presented a second non-parametric test, called the permutation test, for the detection of density dependence in a series of sequential surveys. The test is closely related to the procedure described by Pollard *et al.* (1987), and for this reason I will adopt the same notation as in the previous section. Specifically, we recognize that

$$X_n = X_1 + \Sigma\, d_t, (t = 1, 2, ..., n\text{-}1) \qquad [4]$$

in which d_1, d_2, ..., $d_{n\text{-}1}$constitute a series of random values, with a mean of r under model 1, gradually displacing population size from X_1 to X_n (above). The hypothesis of density independence states that all possible permutations of d_t values are equally likely to occur, resulting in unbounded population changes (i.e., a random walk in density through time). Under model 2, d_t values should occur in such an order that induces the population size to converge on a certain range of densities. As a measure for the amount of fluctuation under H_0 and H_1, the test uses the logarithmic range (L; $X_{max} - X_{min}$) of X_t values. The statistical question here is whether the observed logarithmic range (L_0) calculated from the original sequences of X_t values is significantly smaller than might be expected under random permutations of d_t values (i.e., a density independent population). As for the test of Pollard *et al.* (1987), the statistical distribution of L under H_0 can be assessed by performing a large number of permutations of d_t values, and then calculating L for each retrieved sequence of $X_t$values. The P value is based on the rank of L_0 in the population of L values generated by permutation. Specifically, P equals a/k-1 where a represents the number of L values smaller than or equal to L_0, and k is the number of permutations. P can also be calculated by the Mann-Whitney test (Siegel and Castellan 1988: 128–137) where one of the two samples is L_0 and the other sample is composed of the L values obtained from k permutations.

Applications

In this section, I apply the randomization test and the permutation test to three sets of data, two obtained from the literature and one hypothetical. Field data were from the Avalon caribou herd in Newfoundland (Bergerud 1971; Bergerud *et al.* 1983; Mercer *et al.* 1985; S. Mahoney, pers. comm.) and from the Pukaskwa herd in Ontario (Bergerud 1989; A. T. Bergerud, pers. comm.). The fictitious data set was generated by a computer simulation on the basis of model (2) where $n_0 = 10$, $r = 0.4$, $\beta = 0.9$, and ϵ with a mean of zero and σ of 0.05. Here, my intention is to analyse extremes of population trajectories (Fig. 4), from fluctuations within density bounds (Pukaskwa herd) to unlimited growth (Avalon herd). The hypothetical example illustrates a case of an expanding population for which the respective role of density dependence and environmental vagary on population growth requires statistical assessment (Fig. 4). Population estimates are summarized in Appendix I.

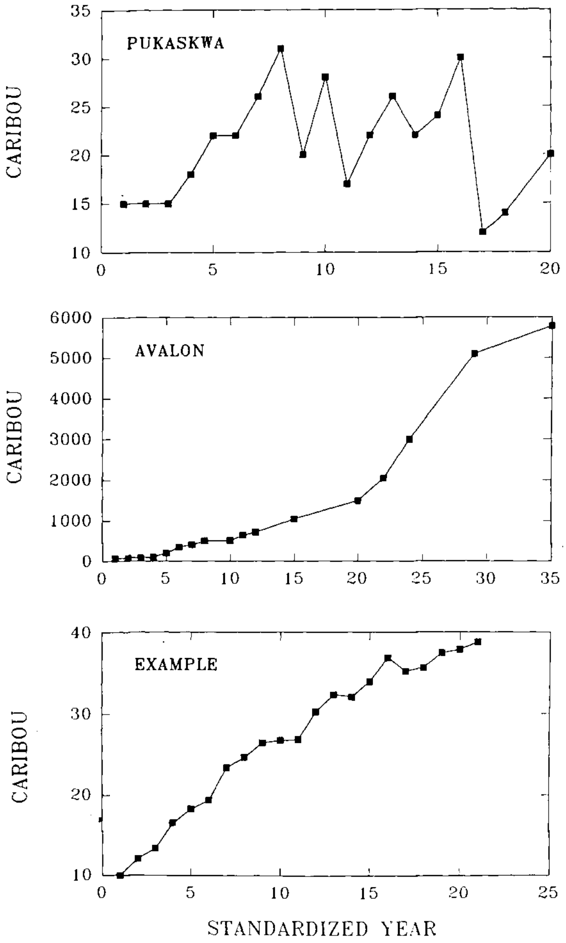

Figure 4. Fluctuations over time of caribou numbers for the Pukaskwa herd in Ontario, the Avalon herd in Newfoundland, and the computer-constructed example.

One minor modification to the randomization test was required to accommodate multiyear censuses. In these cases d_t relative to a multiyear interval was divided by the number of years in that interval to calculate correctly the exponential rate-of-increase. Such modification would affect the variance of d_t values, but not the underlying relationship between d_t and X_t. As the randomization test is a distribution-free statistical analysis (Pollard *et al.* 1987), any differences in the variance among d_t values, when annual and multiannual censuses are treated simultaneously, should not affect the test results. Note, however, that the original d_t values were used to generate the permuted sequences of X_t.

Pukaskwa herd

The Pukaskwa herd ranged from 12 to 31 animals during the period 1972-1991 (Fig. 4). The density independent model was rejected at $P < 0.05$ by both the randomization and the permutation test (Table 1). It is, therefore, quite unlikely that this series of population censuses could have originated simply from random fluctuations. The evidence for density dependence is also reflected by the decline of d_t with X_t (Fig. 5).

Avalon herd

The Avalon herd increased from 71 to 5782 animals during the period 1956-1990 (Fig. 4). Contrary to the previous example, there was a marked trend in the observed data set, typical of a population experiencing unlimited growth. The probability of rejecting the null hypothesis of density independence varied from 0.09 to 0.14 for the randomization test (Table 1). Consequently, the herd may have experienced reduced growth in recent years, but the change was not strongly expressed statistically.

The permutation test gave quite a different result. None of the permuted series of d_t produced a range of X_t values more extreme than that observed in the original sequences of X_t. In fact, this example points to a major weakness of the permutation test; the test loses its power when the population shows a pronounced trend over time. Indeed, when all d_t values are positive, as it is in this example, permutation of d_t values has no effect on the L statistic.

Example herd

The hypothetical example was constructed arbitrarily to mimic a herd recovering from a catastrophic

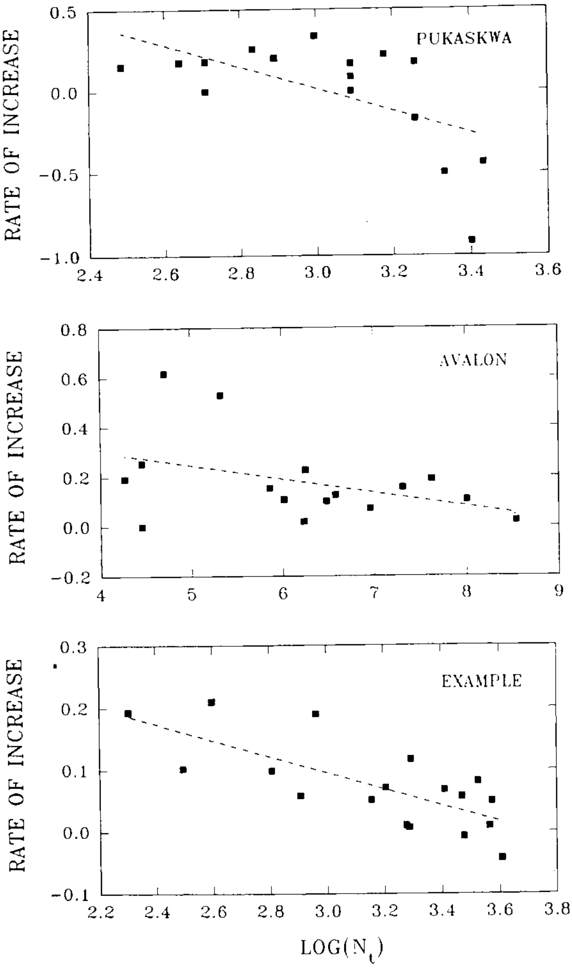

Figure 5. Relationships between the exponential rate-of-increase and log population size for the three populations illustrated in Fig. 4.

reduction in numbers. Population stabilization, in a broad sense, is not readily apparent through inspection of the graphed data (Fig. 4), and inference about density dependence needs to be assessed statistically. The randomization test clearly reveals evidence for density dependence ($P < 0.01$, Table 1). The permutation test, however, is again plagued with low power. The probability to reject H_0 is only 0.77 in spite of a clear trend in declining population growth with population size (Fig. 5). This reinforces the previous statement that the permutation test is largely ineffective when the population undergoes substantial growth without fluctuations around an equilibrium value.

Discussion

Until very recently, assessment of density dependence from a series of population estimates has been hindered by the lack of a suitable statistical procedure. All proposed regression models for which the statistic values under H_0 are set *a priori* (e.g., $b = 0$ or 1) lead to incorrect test results because of biases in the estimator of β (Morris's method, Varley and Gradwell's method), or because of low power when the population undergoes substantial growth or decline (Bulmer's test). Many authors have shown the inefficiency of these procedures (Maelzer 1970; St. Amant 1970; Kuno 1971; Itô 1972; Slade 1977; Royama 1977; Vickery and Nudds 1984; Gaston and Lawton 1987; Pollard *et al.* 1987).

The development of distribution-free, nonparametric tests by Vickery and Nudds (1984, not reviewed here), Pollard *et al.* (1987), and Reddingius and den Boer (1989) represent important contributions to population ecology. In these procedures, the rejection region for the hypothesis of density independence is defined from the data through a computer-assisted randomization process. However, these approaches are not without problems. For example, Pollard *et al.* (1987) showed that the test designed by Vickery and Nudds (1984) was affected by the total displacement in density away from a long-term equilibrium. Pollard *et al.* (1987) further demonstrated that the test proposed by Vickery and Nudds (1984) was related to the randomization test, although with a loss of generality.

The results summarized in Table 1 indicate that the permutation test as proposed by Reddingius and den Boer (1989) is largely inefficient when there is a marked trend in the series of population estimates (e.g., Avalon herd). The permutation test is best only when the study population fluctuates around a long-term equilibrium, such as the Pukaskwa herd. In view of this finding, the conclusion of Reddingius and den Boer (1989) that the permutation test has the same power as the Bulmer's test is not surprising; both tests can be applied with confidence only to a series of censuses showing no trend over time. I concur with Pollard *et al.* (1987) that, at present time, the randomization test appears to be the best available test for detecting density dependence.

Limitations of the randomization test

There are a number of factors that should be considered while interpreting results from the randomization test. I should remark, however, that none of them seem to create systematic biases that would invalidate the procedure.

Measurement errors

Errors of measurement are known to bias the slope of the regression line between d_t and X_t Maelzer

1970; Kuno 1971; Royama 1977). However, such a departure will be present in the slope calculated from the original sequence of X_t, *and* in the slopes obtained from permuted series of X_t. As the randomization test is based on the comparison of b_0 with the distribution of b values computed by permutation, the test results should be relatively insensitive to sampling error. In fact, if we assume that errors of measurement are comparable among X_t values, then the overall variance of X_t (c) amounts simply to the sum of the true variance and the sampling variance. As shown by Pollard *et al.* (1987), the randomization test is not affected by differing values of ϵ, except that high overall variance makes the detection of density dependence more difficult.

Serial correlation in ϵ

An assumption of the randomization test is that ϵ_t be a sequence of independent normally distributed variates, representing the stochasticity element of the system. However, ϵ_t may be subject to serial dependence if, for example,

$$\epsilon_{t+1} = \theta\epsilon_t + \mu_t$$

where $\theta(< 1)$ is the serial correlation constant and μ_t a sequence of independent normally distributed variates. Maelzer (1970) showed that any serial correlation in ϵ_t, and by extension in d_t, biases the regression slope b because changes in X_t no longer follow a first-order autocorrelation model, but instead follow a second-order autocorrelation model (Royama 1977; Reddingius 1990). However, the deviation of b from the true slope β is a function of the sign of the serial correlation parameter (θ); negative values of θ decrease b whereas positive values increase b. A carryover effect of environmental influences, if occurring at all in ungulates (Picton 1984; Messier 1991a), should be associated with positive values of θ. Thus, following a severe winter the rate-of-increase one year later should be somewhat lower than it would have been if the winter had been average. The net result of serial correlation among ϵ_t should, therefore, positively bias b calculated from the original sequence of X_t, but not b values computed from permuted sequences of X_t (because here the serial correlation among ϵ_t vanishes). The above argument suggests that the randomization test would underrate the intensity of density dependence if serial correlation occurs. However, a rejection of H_0 would reinforce the conclusion that density dependent mechanisms actually operate.

Time delay

Often, the rate of population growth at time t is dependent not only on current population size (X_t), but also on some previous population size (X_{t-1}, X_{t-2}, etc.). In these circumstances, fluctuations in animal numbers are not a realization of a piece of first-order Markov chain (Reddingius 1971). The implications of population models that follow a second or upper order process, on the sensitivity of the randomization test, have not been evaluated. Second order process, where d_t is a function of X_t and X_{t-1}, often exhibit cyclic fluctuations in numbers (Royama 1977). This implies that plots of d_t on X_t will be characterised by ellipsoidal (counterclockwise) patterns with various degrees of compression towards the major axis (May *et al.* 1974). Thus, we can safely generalise that the presence of a time delay would restrict the applications of the randomization test because of a poorly defined relationship between d_t and X_t (Itô 1972; Royama 1977; Hanski and Woiwod 1991).

Table 1. Results of the randomization and the permutation test using three statistics (T), when applied to caribou census data of Fig. 4. T were (1) the product-moment correlation coefficient (r_{dx}) and (2) the slope (b) of the regression line between population size (log$_e$-values, X_t) and the exponential rates of growth ($d_t = X_{t+1} - X_t$), and (3) the logarithmic range (L) of X_t values ($X_{max} - X_{min}$). Results include the observed statistic values ($T = r_0$, b_0, and L_0) calculated from the original sequence of X_t values, and the mean statistic values of 500 permutated series of d_t. The estimate of P is also given, i.e., the chance to refute H_0 (density independence hypothesis) while H_0 is actually true.

	Randomization test						Permutation test		
	($T = r_{dx}$)			($T = b$)			($T = L$)		
Caribou herd	r_0	$\bar{r}$	P	b_0	$\bar{b}$	P	L_0	$\bar{L}$	P
Pukaskwa	0.589	0.415	0.06	-0.6741	-0.3530	0.03	0.949	1.436	0.03
Avalon	0.422	0.228	0.14	-0.0551	-0.0067	0.09	4.400	4.400	1.00
Example	0.762	0.197	® 0.01	-0.1299	-0.0119	® 0.01	1.354	1.361	0.77

Linear model

Pollard *et al.* (1987) developed their statistical procedure with the assumption that the relationship between d_t and X_t is linear. However, I suspect, without presenting a proof, that the randomization test can be applied on the basis of a curvilinear model when inspection of residuals along the regression line reveals a poor fit (e.g., Pukaskwa herd, Fig. 5). As for the linear model, r_{dx} of the curvilinear regression model (more appropriately R_{dx}) calculated from the original sequence of X_t, can be compared with R values obtained from permuted sequences of d_t. Here, the hypothesis of density independence should imply that all correlation constants (β_1, β_2, etc.) equal zero, assuming infinite sample sizes. For example, applying a quadratic model to the Pukaskwa data (Fig. 5) appreciably improves the fit (R_{dx} = 0.82, compared to 0.59 for the linear model), with a rejection of H_0 at $P < 0.01$.

Final remarks

Density dependence is achieved by a complex of factors whose collective action creates bounded population fluctuations (Berryman *et al.* 1987; Berryman 1991; DeAngelis and Waterhouse 1987). The question is not whether density dependence exists, for without it, the recognised persistence of most natural populations would be inexplicable (Royama 1977). Rather, the goal is to assess (1) in what range of densities do feedback mechanisms operate, and (2) what are the population processes involved? Any test of density dependence based on a series of census data cannot address the later question. For example, the abrupt decline in the rate-of-increase of the Pukaskwa herd at elevated densities (Fig. 5) may be due to food competition, emigration, or some form of interaction between the two factors. An appropriate test, however, would differentiate between a period of unlimited growth and a period during which mechanisms of population regulation are instrumental in stabilizing numbers.

Unlimited growth, often associated with a given range of densities, does not imply that prevailing population processes are largely density-uninfluenced. It is important to stress that two density-influenced factors may have antagonistic actions on population growth. For example, at Isle Royale, wolf predation and food competition exert opposite influences on moose during periods of moderate density (Messier 1991a). The net effect of two population processes with opposite actions is to make the rate-of-increase largely insensitive to changes in density (i.e., weak density dependence), a type of interaction associated with the unnecessary concept of "density-vague" population regulation (Strong 1984, 1986).

Some ecologists object to the notion of "equilibrium" that underlies most tests of density dependence (Wolda 1989). A long-term equilibrium density is simply a mathematical abstraction illustrating the fact that a population trajectory over time would tend to converge toward that equilibrium (Berryman 1991). The modern view of population dynamics recognises the lability of equilibrium points due to stochastic effects, and the fact that equilibria can be unstable or multiple (DeAngelis and Waterhouse 1987; Berryman *et al.* 1987; Sinclair 1989). In that perspective, one of the basic questions in studies of population dynamics is not simply to determine whether the density of animals is regulated or not, but to assess the relative importance of density-dependent and density-independent processes in changes of population size over time (Schaefer and Messier 1991).

Acknowledgements

The Natural Sciences and Engineering Research Council of Canada supported my work through a University Research Fellowship and an operating grant for computer analyses. B. R. Neal and J. A. Virgl provided critical comments on the manuscript.

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Appendix I

Summary of caribou census data for the Pukaskwa herd in Ontario (Bergerud 1989, A. T. Bergerud pers. comm.) and the Avalon herd in Newfoundland (Bergerud 1971, Bergerud *et al.* 1983, Mercer *et al.* 1985, and S. Mahoney pers. comm.). Data for a hypothetical example mimicking an expanding herd are also summarized.

Pukaskwa		Avalon		Example	
N	Year	*N*	Year	*N*	Year
15	1972	71	1956	10.0	1
15	1973	86	1957	12.1	2
15	1974	111	1958	13.4	3
18	1975	206	1959	16.6	4
22	1976	350	1961	18.3	5
22	1977	409	1962	19.4	6
26	1978	508	1964	23.4	7
31	1979	518	1965	24.7	8
20	1980	650	1966	26.5	9
28	1981	720	1967	26.8	10
17	1982	1050#	1970	26.9	11
22	1983	1500#	1975	30.3	12
26	1984	2050#	1977	32.4	13
22	1985	3000	1979	32.1	14
24	1986	5099	1984	34.0	15
30	1987	5782	1990	36.9	16
12	1988			35.3	17
14	1989			35.7	18
20	1991			37.5	19
				37.9	20
				38.8	21

Estimated from Fig. 2 of Bergerud *et al.* 1983.

Printed from manuscript after editorial review.

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Predation and caribou populations

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Abstract: Predation, especially wolf *(Canis lupus)* predation, limits many North American caribou *(Rangifer tarandus)* populations below the density that food resources could sustain. The impact of predation depends on the parameters for the functional and numerical response of the wolves, relative to the potential annual increment of the caribou population. Differences in predator-avoidance strategies largely explain the major differences in caribou densities that occur naturally in North America. Caribou migrations that spatially separate caribou from wolves allow relatively high densities of caribou to survive. Non-migratory caribou that live in areas where wolf populations are sustained by alternate prey can be eliminated by wolf predation.

Keywords: Caribou, wolves, predator-prey relationships, population dynamics.

Rangifer, Special Issue No. 7: 46—52

Caribou populations without predators

In the absence of major predators or high levels of human harvest, caribou and reindeer *(Rangifer tarandus)* populations generally increase until their populations become regulated by density-dependent competition for food (Klein 1968, Leader-Williams 1980, Skogland 1985). Competition for food results in reduced nutrient intake due to lower forage intake rates and reduced diet quality as less nutritious food items are incorporated into the diet (White 1983). Energy expenditures for movement and cratering may also increase as it becomes more difficult to obtain food. Decreased nutrient intake and increased energy costs lead to a reduced pregnancy rate, low calf survival and higher adult mortality rates in *Rangifer* populations (Leader-Williams 1980, Skogland 1985, Messier *et al.* 1988, Thomas 1982).

Density-dependent competition results in a dome-shaped annual increment curve (Caughley 1977) (Fig. 1). At low densities, annual increment is small because although there is little competition and the population growth rate is high, there is a small breeding population. The maximum annual increment occurs at an intermediate density where there is a moderate sized breeding population and the growth rate is still relatively high because competition is not yet severe. At high densities, annual increment again becomes small because despite an abundant breeding population, the growth rate is low due to density-dependent competition for resources. In the absence of predators or harvesting, the population will generally increase until competition for resources reduces the growth rate and annual increment to zero. *Rangifer* populations regulated by competition for food resources often attain densities exceeding $2/km^2$ (Table 1).

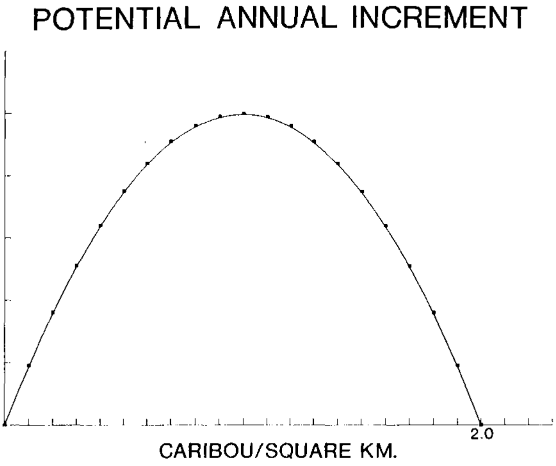

Fig. 1. Annual increment curve for caribou populations in absence of major predators or human harvest.

Predator-prey dynamics

When predators are present, especially wolves *(Canis lupus)*, caribou populations are often reduced below the density that food resources could sustain. The predation rate depends on the number of predators and the number of prey killed by each predator. In general, the number of predators (numerical response) and the number of prey killed by each predator (functional response) will change as a function of prey density (Holling 1959). The number of prey killed/predator will initially increase with prey density as prey become easier to find but will eventually reach a plateau as each predator becomes satiated (Fig. 2b). Various numerical responses are possible (Fig. 2c). The number of predators may increase with prey density if the predator population is limited by availability of the prey species of interest (Fig. 2c, line a). At high prey densities, the numerical response may reach a plateau if some factor other than availability of the prey species of interest begins to limit predator population growth (Fig. 2c, line b). If the predator population is regulated by availability of some other prey species or limiting factor, there may be no numerical response of predators to changes in density of the prey species of interest (Fig. 2c, line c). The functional and numerical response of predators to changes in caribou density have not been quantified. However, Messier and Crete (1985) demonstrated that wolves had a higher rate of consumption and reached higher densities in an area of high moose *(Alces alces)* density compared to areas of low moose density. Fuller (1989) summarized data from numerous studies of wolves to demonstrate the numerical response of wolves to increasing prey densities.

The number of prey killed by predators is the product of the number of predators and the number of prey killed by each predator (Fig. 2a). In general, few prey will be killed when they are at low densities because predators will also be at low numbers and the sparse prey are very difficult to find. As prey densities increase, the number of prey killed may increase exponentially due to the multiplicative effect of an increasing numerical and functional response of predators. If either the functional or numerical response levels off, the number of prey killed will increase linearly with prey density. If both the numerical and functional response level off, the number of prey killed will remain constant with further increases in prey density. Consequently, the predation rate (proportion of prey killed) will often be density-dependent at low prey densities, density-independent at intermediate prey densities and inversely density-dependent (depensatory) at high prey densities.

The impact of predation depends on the magnitude of predation losses compared to the potential annual increment that the prey population would produce in the absence of predation (Fig. 1). If losses to predation exceed the potential annual increment, the prey population will decline. If losses to predation are less than the potential annual increment,

Table 1. Density of *Rangifer* populations in relation to the level of predation.

Category	Location	Density	Source
Major predators rare or absent	Slate islands	4–8/km^2	Bergerud 1983
	Norway	3–4/km^2	Skogland 1985
	Newfoundland (winter range)	8.9/km^2	Fong *et al.* 1991
	South Georgia	2.0/km^2	Williams and Heard 1986[a]
Migratory Arctic herd	George River	1.1/km^2	Messier *et al.* 1988
	Porcupine	0.6/km^2	Williams and Heard 1986
	Northwest Territories	0.6/km^2	Williams and Heard 1986
Mountain dwelling herds	Finlayson	0.15/km^2	Farnell and McDonald 1987
	Little Rancheria	0.1/km^2	Farnell and McDonald 1990
	Central Alaska	0.2/km^2	Williams and Heard 1986
Forest dwelling herds	Quesnel Lake	0.03/km^2	Seip 1991
	Ontario	0.03/km^2	Williams and Heard 1986
	Saskatchewan	0.03/km^2	T. Rock, pers comm

[a] Densities calculated from data presented in Williams and Heard 1986

the prey population will increase, although more slowly than if predators were absent. The prey population will stabilize at a density where losses to predation equal the potential annual increment. Time lags and variations in density-independent limiting factors will cause fluctuations around the equilibrium density.

Migratory Arctic caribou

A high prey-predator equilibrium will occur when the number of prey killed by predators increases slowly as a function of prey density relative to the annual increment curve (Figure 2). That situation will occur when the prey have an effective anti-predator strategy or when the capacity of the predator population to respond to increasing prey is limited by other factors. The prey population will be regulated by the combined density-dependent effects of predation and competition for resources. It appears that many migratory Arctic caribou populations exist at a high prey-predator equilibrium. Wolf predation is usually a major limiting factor, especially of calves (Miller and Broughton 1974, Whitten *et al.* 1988), but caribou remain abundant and can sustain a substantial human harvest. It appears that migratory Arctic caribou populations are able to reach a high prey-predator equilibrium because their annual migrations are an effective anti-predator strategy. Arctic wolves are sustained almost exclusively by caribou (Kuyt 1972). However, the capacity for wolf numbers to increase in response to increasing caribou numbers is severely limited by the long distance migrations of the caribou. Reproductive wolves are restricted to the area near the den during summer months. Most wolves den near treeline and few den near the calving grounds (Heard and Williams 1991). Consequently, most wolves are unable to prey on caribou on the calving grounds. Also, most of the wolves are unable to take advantage of increasing numbers of caribou to feed their pups during the denning period so the numerical response of wolves to increasing caribou numbers is greatly limited.

In some cases, the numerical response of predators is so limited that Arctic caribou populations essentially escape any significant limitation due to predators and caribou increase until they are regulated primarily by competition for food (Fig. 3). This situation has been reported for the George River ca-

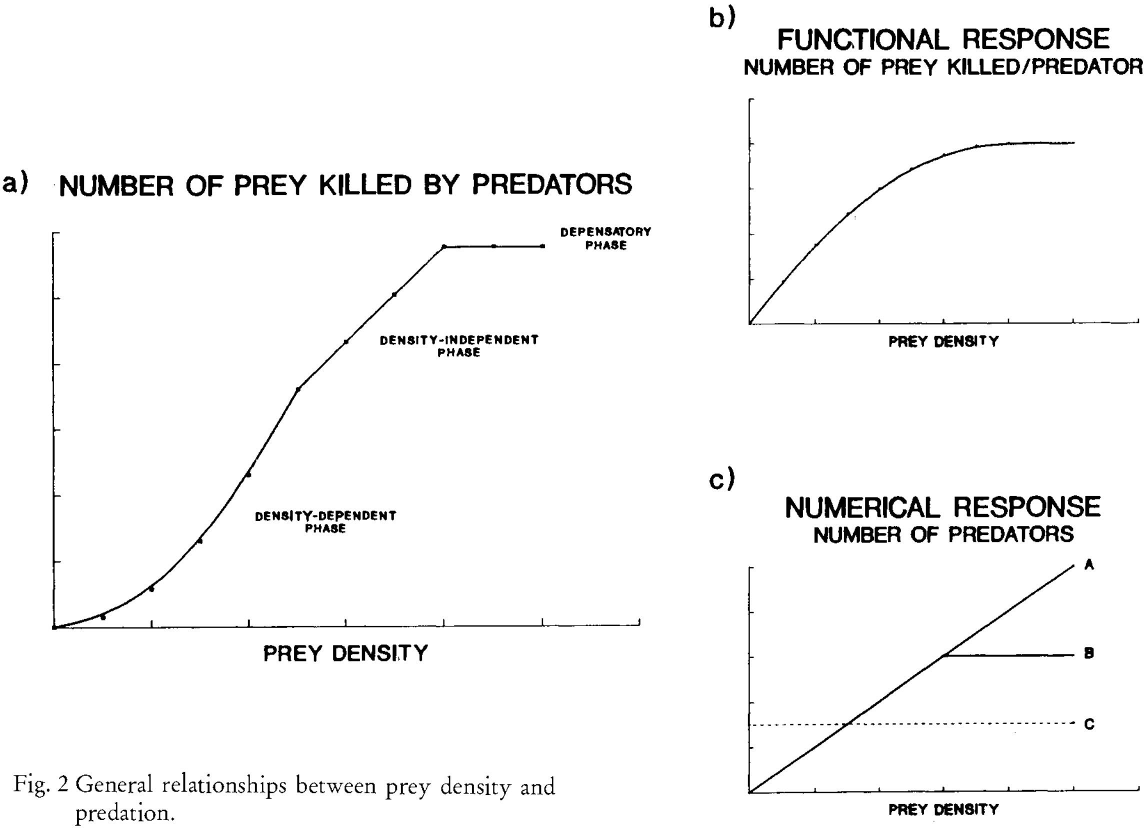

Fig. 2 General relationships between prey density and predation.

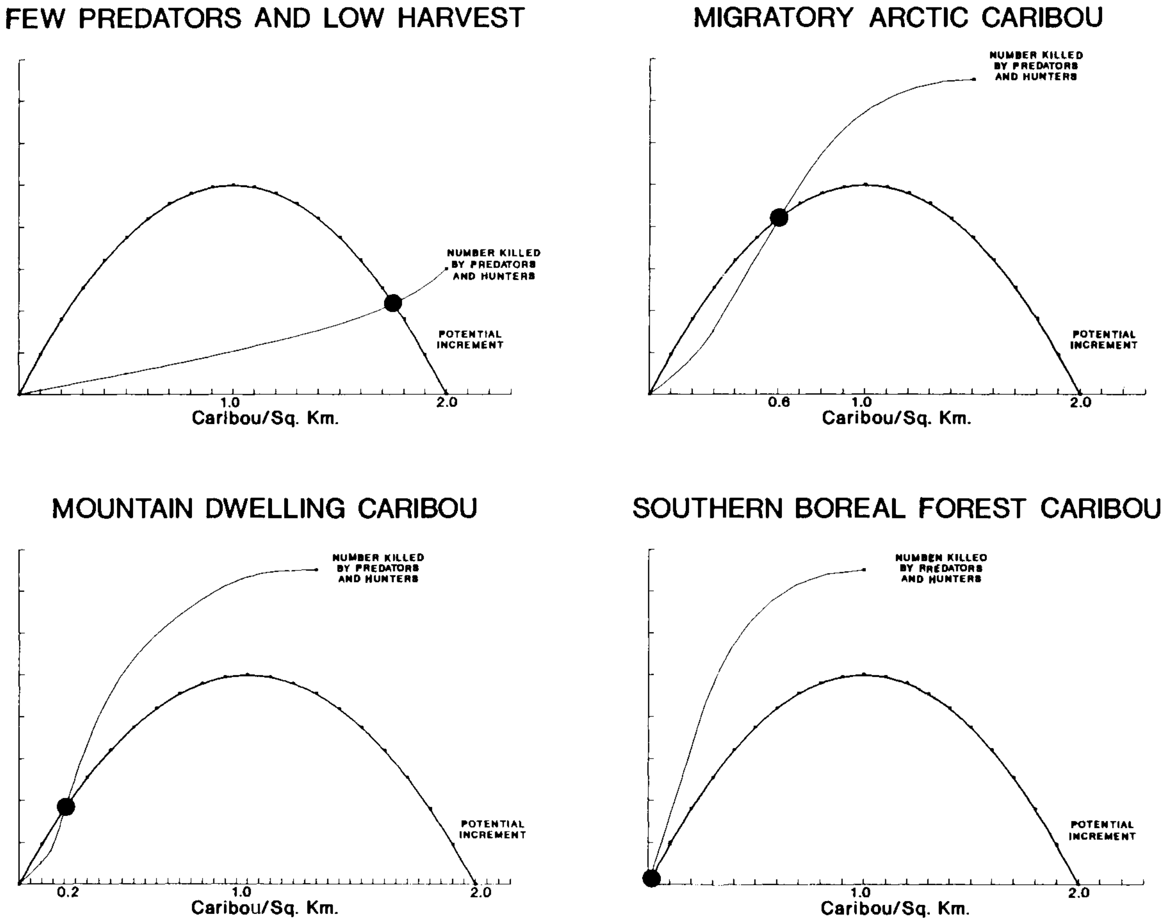

Fig. 3. General predator-prey relationships for caribou populations in different areas of North America. The ● indicates the point of predator-prey equilibrium.

ribou herd in northern Quebec which attained a density of about 1/km^2 (Messier *et al.* 1988). A high mortality rate of wolves and a low human harvest of caribou will increase the likelihood that migratory Arctic caribou will escape from being regulated by predation.

In other cases, predation rate and human harvest rate appear to be adequate to restrict the growth of Arctic caribou herds before competition for food becomes extreme (Fig. 3). Many barren-ground caribou herds in northern Canada and Alaska appear to have a medium prey-predator equilibrium at densities of about 0.6/km^2 (Table 1). Wolf predation is more likely to regulate Arctic caribou populations at a medium density if wolves are reasonably abundant and there is also a significant human harvest on caribou. Caribou herds at a medium prey-predator equilibrium density would exhibit some nutritional stress due to competition for food but predation and human harvest would be the primary limiting factors. This situation is probably the ideal case for management because caribou are abundant and in good physical condition, natural predator populations are present and the herd is providing a sustainable harvest for human use. The population is also easily subject to management by modified harvest levels or wolf control. In contrast, high density, food regulated caribou populations are vulnerable to major population crashes (Klein 1968). Adequate predator populations should be maintained and appropriate human harvest levels should be encouraged to prevent excessive growth of caribou populations. Otherwise, caribou populations may increase so rapidly that they cannot be effectively managed and become susceptible to catastrophic population crashes.

Forest-dwelling caribou

A low prey-predator equilibrium will occur when the number of prey killed by predators increases rapidly as a function of prey density relative to the annual increment curve (Fig. 3). That situation will occur when the prey lack an effective anti-predator strategy or when predators are sustained by alternate prey species even when the prey species of interest is at low densities. Caribou populations below treeline in North America are more vulnerable to wolf predation than Arctic caribou because wolf populations are maintained by a variety of prey species and the caribou do not have long-distance migrations to space themselves away from wolves. Also, other predators such as bears (*Ursus* spp.) are more abundant than in Arctic areas and remove an additional component of the annual increment. Wolf populations are sustained by a variety of prey species including caribou, moose, mountain sheep (*Ovis* spp.), elk *(Cervus elaphus)* and deer (*Odocoileus* spp.). Therefore, wolf numbers can remain high even if predation has drastically reduced one of the prey species. Increases in the abundance of one of the prey species may support increased wolf numbers and thereby have deleterious effects on one or more of the other prey species. Caribou are extremely vulnerable to wolf predation compared to most other ungulate species. They are unable to fight off predators the way moose can, they do not use escape terrain like mountain sheep and mountain goats *(Oreamnos americana)*, and they have a low reproductive rate compared to most other ungulates such as deer so they cannot sustain high levels of predation. Therefore, caribou populations are usually the most vulnerable species in multiple prey-predator systems. Wolf predation can eliminate caribou from areas where the wolf population is sustained by other prey species because there is no negative feedback on the number of wolves as caribou decline (Seip 1991).

Woodland caribou in the mountainous regions of Yukon, Alaska and northern British Columbia are usually able to co-exist with wolves, bears and alternate prey species such as moose. Although major declines have occurred in some areas, possibly due to increases in moose numbers and/or excessive human harvest (Bergerud 1974), viable populations of caribou continue to survive at densities of about 0.2/km^2 (Table 1, Fig. 3). Seasonal migrations of caribou to alpine areas and habitat segregation between different ungulates species generally results in sufficient spatial separation from wolves and alternate prey to allow caribou populations to persist (Bergerud *et al.* 1983, Seip 1990). However, predation and human harvest are usually the primary limiting factors so caribou populations in those mountainous regions respond quickly to changes in the harvest rate and use of wolf control (Gasaway *et al.* 1983, Farnell and McDonald 1988, Bergerud and Elliot 1986).

It appears that caribou populations in the boreal forests of North America historically co-existed with wolves at a low prey-predator strategy (Bergerud and Page 1987). By spacing out and living at low densities, caribou reduce the predation rate by becoming difficult for predators to find. Living at low densities can reduce both the functional and numerical response of predators. However, that anti-predator strategy is only effective if caribou are the primary prey species in the area.

Forest-dwelling caribou populations throughout North America have undergone major declines during the 1900's (Bergerud 1974). Wolf predation and human harvest have been implicated as the major cause of many of those declines. Increased wolf predation on forest-dwelling caribou populations appears to be related to the range expansion of moose in North America (Bergerud 1974, Seip 1990). Moose expanded their range during the 1900's, especially in northern Ontario, British Columbia, Yukon and Alaska (Peterson 1955). The colonization of moose was followed by reports of declining caribou populations in many of those areas (Edwards 1956, Darby *et al.* 1989). The presence of moose provided an alternate prey which sustains increased wolf numbers (Seip 1991). The increased wolf population results in an increased predation rate on caribou and declining caribou numbers (Seip 1991). Because the predator population is sustained primarily by moose, it is possible for the wolves to totally eliminate the caribou population without any decline in wolf numbers (Fig. 3).

Forest-dwelling caribou have declined or been eliminated from large parts of their historic range in northern Ontario, Saskatchewan, Alberta and non-mountainous regions of British columbia. Caribou densities of 0.03/km^2 are common for remnant herds (Table 1) but many of those herds are continuing to decline to extinction. Only caribou which have a predator-avoidance strategy such as calving on islands (Cumming and Beange 1987) or caribou in the extreme north of the boreal forest where moose and human harvest are less common appear to be able to maintain their populations.

Unless wolf control and/or reduction of moose populations is undertaken, caribou will probably continue to disappear from much of their historic range in the southern part of the boreal forest. Any habitat modifications, such as fires, which enhance populations of moose or other prey species are likely to accelerate the decline of caribou. Also, any reduction in caribou habitat resulting from logging or fire will concentrate the remaining caribou into the remaining area and effectively increase their density. That reduction in their ability to space out makes it easier for predators to locate them and will also contribute to a more rapid decline. Roads may also improve access to caribou for predators and hunters.

Summary

Numerous limiting factors including winter severity, insect harassment, diet quality and accidents undoubtedly have an impact on caribou populations and result in year to year (primarily density independent) fluctuations in caribou populations. However, when wolves are present, it appears that wolf predation is the dominant, natural regulating factor. Differences in the effectiveness of predator-avoidance strategies appear to explain the major differences in caribou density that occur naturally in different regions of North America. Caribou generally appear unable to survive in areas where there is extensive overlap with wolves and alternate prey species. Caribou populations rely on migrations to become spatially separated from wolves or spacing out and living at low densities to minimize the predation rate. The number of caribou in an area depends on the effectiveness of those strategies at avoiding predators.

For migratory caribou in Arctic areas, manipulation of predator numbers and human harvest rates can be used to maintain abundant caribou populations while preventing excessive population growth that increases the risk of catastrophic population crashes. In forested habitats, in addition to managing predator numbers and harvest rates, habitat management is also important. Habitat changes which enhance alternate prey species or a reduction in habitat which concentrates the caribou and increases their density may undermine their predator avoidance strategies and lead to increased predation rates.

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Printed from manuscript after editorial review.

The implications of environmental variability on caribou demography: theoretical considerations

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Abstract: Random environmental influences, such as snow cover, are widely regarded as an integral feature of caribou population dynamics. We conducted computer simulations to explore the ramifications of such stochastic variability for caribou demography. We devised 4 models with increasing levels of complexity: Model 1, density-independence under different levels of stochasticity and r; Model 2, non-linear effect of snow cover on r; Model 3, non-linear effect of snow cover on r and stochasticity as a function of population size; and Model 4, non-linear effect of snow cover on r, stochasticity as a funciton of population size, and density-dependence according to the logistic equation. The results of Model 1 indicated that nearly all caribou populations subject only to environmental vagaries experienced either extincition or irruption. Model 2 revealed that non-linear effect of snow cover depressed the realised r as a function of population size. Finally, Model 4 suggested long-term population as previously reported in literature, but with reduced chance of overshooting K under moderate to high environmental variability.

Keywords: caribou demography, computer simulation, environmental variability, population dynamics.

Rangifer, Special Issue No. 7: 53—59

Introduction

One of the axioms of population biology is that virtually no population fluctuates solely as a function of its density (Strong 1986). Indeed, random environmental changes, such as snow cover, are widely regarded as a prominent part of the population dynamics of caribou (Klein 1968, Reimers 1977, Gates *et al.* 1986, Melgaard 1986, Schaefer and Pruitt 1991). One approach to the study of environmental effects on population change is to control such effects either experimentally (e.g., Ollason 1977) or statistically (e.g., Botsworth 1985, Mech *et al.* 1987, Messier 1991a). A complementary approach is to construct strategic models (Nisbet and Gurney 1982) to generate new hypotheses.

Here, we report on the results of a series of such computer simulations to explore the ramifications of environmental vagaries on caribou demography. We began with a simple model of pure density-independence (Model 1) into which we incorporated increasing levels of complexity (Models 2-4). Our models are simple (there is no age structure, for example), and thus it is the qualitative results that were of interest, inasmuch as they might be of heuristic value.

All simulations were conducted with SIMCON software (D. Vales and C.J. Walters, Univ. British Columbia, Vancouver, B.C.) using QuickBasic version 4.5 (MicroSoft Corp., Redmond, VA).

Model 1: Density-independence

We began by simulating each model population through a simple, unlimited random walk. For each replicate population projected over 1000 years, we specified a mean value of r and a stochasticity factor in standard deviation (SD) units (Fig. 1). Fluctuations on r were normally distributed about the mean, with a SD varying from 0 to 0.5 of r_{MAX} (0.25). N_0 was 50 for all cases. For each combination of r and SD, we calculated the likelihoods of extinction ($N < 1$) and irruption ($N > 1000$) for 1000 replicate populations.

The results indicated that the probabilities of extinciton and irruption were sensitive to both

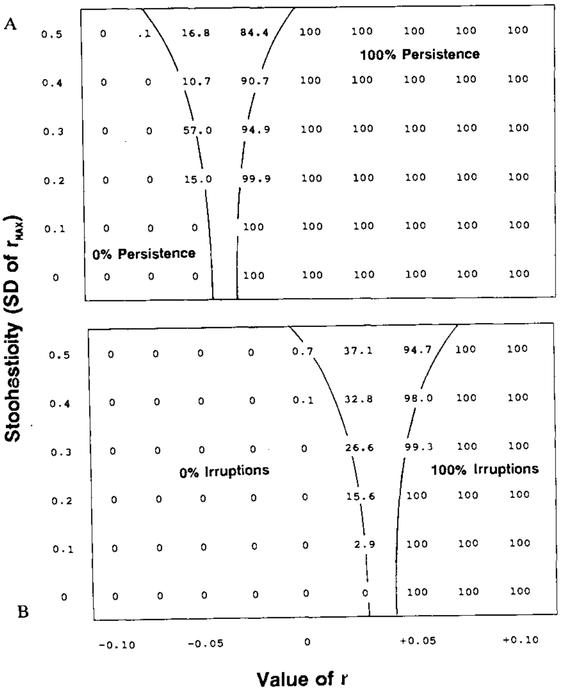

Figure 1. Probabilities (%) of (A) persistence ($N > 1$) and (B) irruption ($N > 1000$) under various combinations of *r* and stochasticity. Each datum represents 1000 replicate populations projected over 1000 years ($N_0=50$) specific to each combination of mean *r* value and SD. The full model was $N_{t+1} = N_t e^r$ where N represented population size, and *r* was a normally-distributed growth rate with a mean varying from - 0.10 to + 0.10 and a SD varying from 0 to 0.5 of r_{MAX} (0.25).

r and stochasticity (Fig. 1). At low intrinsic growth rates, most populations were unable to persist; at high growth rates, persistence rates improved but most of these populations also irrupted. Persistence and irruption probabilities were more sensitive to stochasticity at intermediate *r* levels (-0.03 to + 0.03).

Our results are consistent with earlier models (Leigh 1981, Belovsky 1987, Goodman 1987, Pimm *et al.* 1988, 1989) that persistence times increase with increasing *r* and with decreasing magnitude of temporal fluctuations. Pimm *et al.* (1988) confirmed these hypotheses empirically in a study of extinction rates of British birds.

These results further underline the distinction between factors which are *limiting*, producing annual fluctuations in density, and those which are *regulating*, maintaining densities within reasonable bounds (Murray 1982, Fowler 1987, Messier 1991a,b). Regulating factors generate stabilisation of animal numbers and are necessary to ensure the numerical persistence of population. Our results reinforce the idea that in a solely density-independent world, any level of stochasticity, however slight, will ultimately cause population extinction or explosion.

This argument was recognised intuitively by Reddings (1971) and Strong (1986). These authors, while conceding its logic, countered by noting that it focuses on the ultimate result following an infinite amount of time. Thus Reddingus (1971:37) wrote: «It can never be observed that animal populations persist forever». Nontheless, the narrow margin between extinction and unrealistic densities (compare Fig. 1A and IB) implies that unbounded random walks are inadequate models for animal populations. Some form of density-dependence, or ceiling on density-independence («density-vagueness» of Strong 1984, 1986), is required for long-term population persistence.

Model 2: Non-linear effect of snow cover

In Model 1, we applied variability to *r* directly. In this and subsequent models, we specified a relationship between *r* and a random variable, snow cover. In particular, we visualised an ever-decreasing function such that each increment of snow accumulation had an increasingly depressing effect on *r* (Fig. 2.). Snow cover was normally-distributed random variable (mean = 1, SD = 0.5). The postulated function (Fig. 2) was associated with a deterministic rate of growth

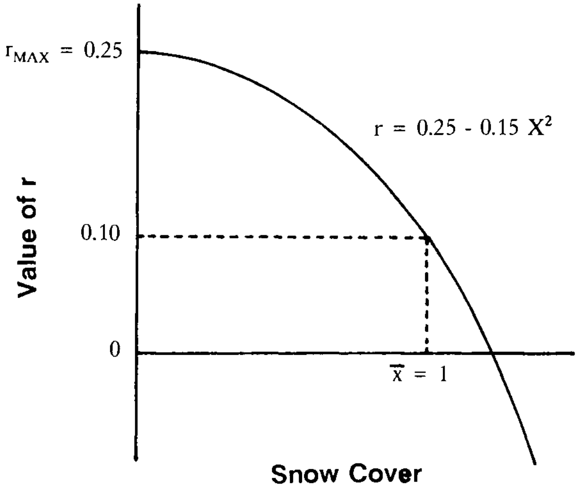

Figure 2. Hypothesised non-linear relationship between *r* and snow cover for Model 2. Snow cover values were normally distributed, with a mean of 1 and SD of 0.5.

(r_{DET}) of 0.10 for average snow cover, and r_{MAX} of 0.25 with no snow. These values were within the range of possible values reported in the literature for *Rangifer* (Bergerud 1980).

Although snow cover varied symmetrically about its mean, caribou population growth did not. Year-to-year variations in snow cover generated an average r value lower than that without variation. This was due to the non-linear relationship: an increment in snow cover above the mean negatively affected population growth more than the converse situation. Thus, the mean exponential rate of increase (r = 0.06) with environmental variability was lower with than the deterministic r-value (r_{DET}= 0.10) under a constant environment (Fig. 3A). Consistent with this realised r, populations typically irrupted (Fig. 3B).

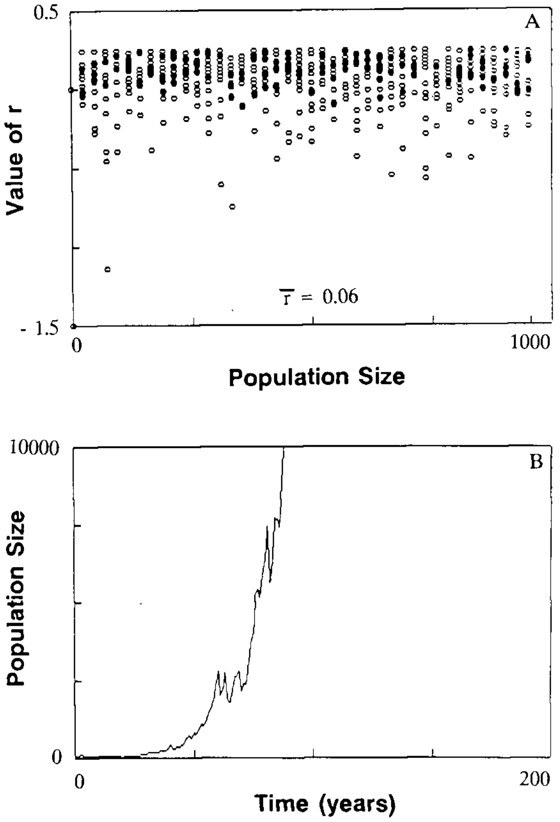

Figure 3. (A) Realised values of r at various densities as generated by Model 2. The full model was $N_{t+1} = N_t e^{r(s)}$ where N represented population size and r (population growth rate) was a stochastic function of snow as depicted in Fig. 2. (B) Typical trajectory of a population under Model 2.

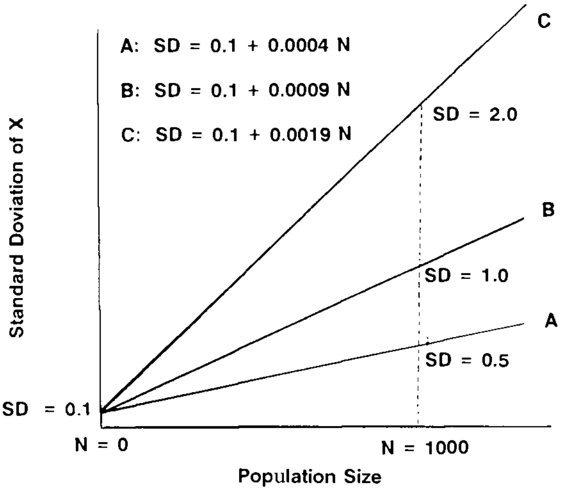

Figure 4. Hypothesised relationship between the level of stochasticity (SD of snow cover effect, X) and population size for (A) low, (B) medium, and (C) high levels of stochasticity.

This depression on population growth due to environmental variability accords with previous models of the demography of large, tropical herbivores. Van Sickle (1990) assumed that rainfall determined calf survival of African ungulates and found that long-term rates of population growth declined whenever such random variation was applied. Similarly, Caughley (1987) noted that symmetrical deviations in pasture biomass (driven by rainfall) produced a mean density of kangaroos lower than that in the absence of environmental variability. He hypothesised an analogous non-linear numerical response of the animals to an environmental parameter (pasture biomass) as we suggested in Fig 2. A discrepancy in deterministic and realised values, due to variability, is characteristic of such concave-down funtions (Rubenstein 1982).

Model 3: Non-linear effect of snow cover, and stochasticity as a function of animal density

Here, we extended Model 2, We retained the non-linear relationship between snow cover and population growth (Fig. 2) and visualised a level of stochasticity as a linear function of population size (Fig. 4) rather than being fixed (i.e., SD of snow = 0.5) as in Model 2. We explored three levels of such stochastic change, submodels A, B and C, each with increasing slopes of the stochasticity-density function.

What is the biological basis for this relationship between the level of stochasticity and density? We hypothesise that a higher population levels, cratering by caribou may exacerbate the effect of snow cover such that subsequent foraging is impeded. This hypothesis follows Pruitt (1959) who noted the biologically important alteration in snow cover due to caribou cratering; consequently, animals typically do not excavate for terrestrial lichens more than twice in a given area. Figure 4 implies an interaction between the variability of the effect of snow cover and population densities of caribou. We hypothesise that food availability (not to be confused with food abundance) is a negative function of cratering intensity in a given environment. Caughley (1987) also reported a greater coefficient of variability for vegetation biomass in the presence of high numbers of kangaroos than in their absence.

As in Model 2, realised *r*-values were depressed compared to a deterministic *r*-value of 0.10. Here, however, the two facets of Model 3 combined such that population growth was density-dependent. At low densities (*N* = 50), values close to r_{DET} were attained because environmentally-induced variability in *r* was minimal. At the other extreme (*N* = 1000), depression of the population growth rate was greater for all three submodels (Fig 5). As expected, this decline was most severe for the high stochasticity submodel (Fig. 5C). This density-dependence, related to environmental variability, was reflected in the population trajectories (Fig. 6). Populations tended to persist within density bounds, often with precipitous declines from high densities. The high stochasticity submodel was characterised by lower densities and an apparently higher probability of extinction (Fig. 6C) due to the elevated chance of successive low values of *r* (Fig. 5C). We noted, however, that most population trajectories did not reveal predictable cyclicity in animal numbers.

The density relationships depicted in Fig. 5 are similar to Strong's (1986:260) «spreading scatters», a correlated mean and variance of *r*. Strong suggested that under such a scenario, populations will experience density-vagueness, i.e., density-dependent feedback only at high densities. Below some ceiling, fluctuations will be largely random, driven by stochastic effects. Although the magnitude of population declines was greater at higher densities (Fig. 6), population growth declined predictably with *N* (Fig. 5). Thus, the appearance of density-vagueness may simply coincide with a lack of detectability of regulating processes at low densities.

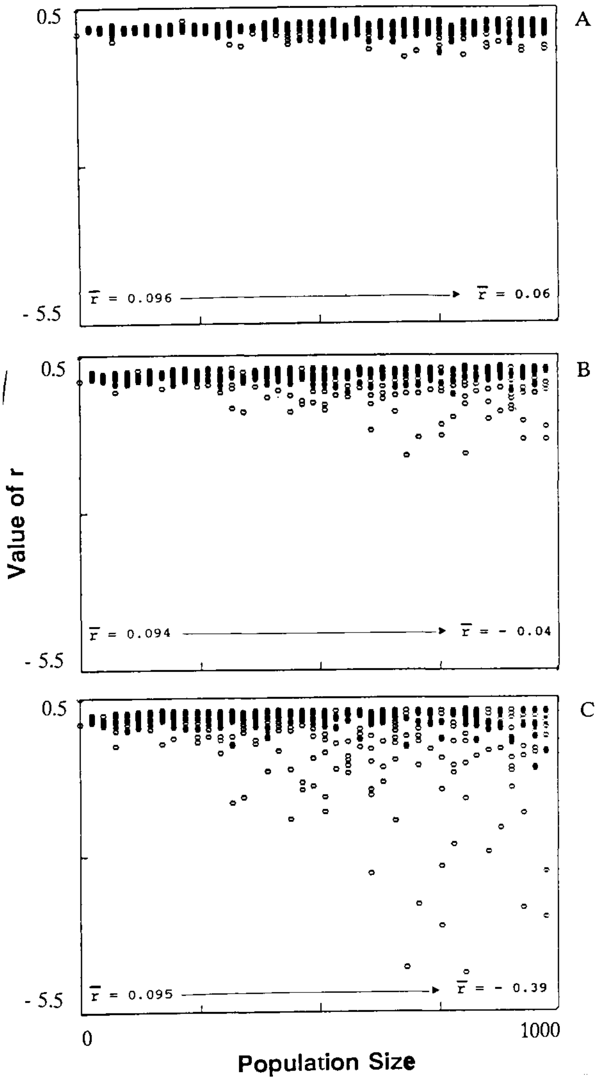

Figure 5. Realised values of *r* at various densities as generated by Model 3 for (A) low, (B) medium, and (C) high levels of stochasticity. Average *r*-values at N = 50 and N = 1000 are presented at the bottom of each panel to illustrate the predictable decline of *r* with increasing population size. The full model was $N_{t+1} = N_t e^{r(s,N)}$ where N represented population size, and *r* (the population growth rate) was a stochastic function of snow cover effect as influenced by caribou numbers (see Fig. 2, 4). With no environmental variability, *r* was fixed at 0.10.

The decline in the growth rate of hypothetical populations, with increasing environmental variance, has been noted elsewhere (Tuljapurkar and Orzack 1980, Van Sickle 1990). If environmental variability increases with population size (as we hypothesise), then our results imply that population regulation can be attained, specifically because the non-linear function depicted in Fig. 2 becomes more instrumental in depressing r at high population densities. In effect, the two components of Model 3 (the non-linear effect of snow and increasing variability with density) alter the year-to-year carrying capacity for caribou. This may fit Strong's (1986) notion of «liberal» population regulation where density bounds are unlikely to be static. Finally, our model is qualitatively consistent with observations of Meldgaard (1986) who noted that long-term population fluctuations of Greenland caribou were often dramatic, occasionally terminating in extinction.

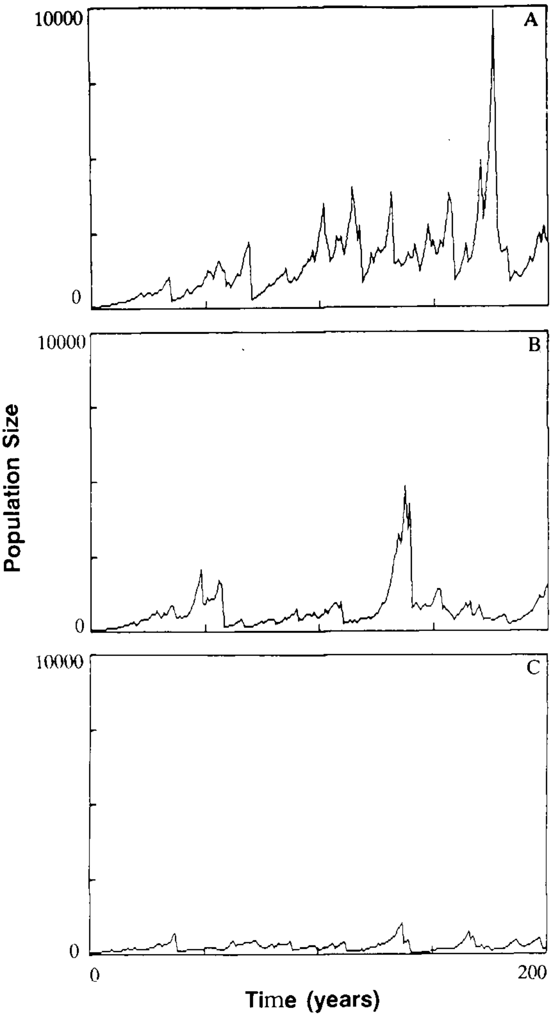

Figure 6. Typical trajectories for population under Model 3 for (A) low, (B) medium, and (C) high levels of stochasticity.

Model 4: Non-linear effect of snow cover, stochasticity as a function of animal density, and density-dependent logistic growth

Next, we explored the behaviour of hypothetical populations when our stochastic model was incorporated into a traditional logistic model. Model 4 thus specified two sources of depression on r: that caused by snow cover (Model 3) and that due to the logistic growth equation. We used a moderate level of stochasticity (equation B of Fig. 4), set carrying capacity without snow (K) at 400, and included 20-year time delay (T) in the logistic growth equation as hypothesised by Messier *et al.* (1988). A r_{DET} of 0.10 and T of 20 resulted in density peak of $3K$ for each population cycle (Fig. 7A) as previously reported by Messier *et al.* (1988).

The results of our simulations were variable. In some trajectories, the underlying cyclicity (typical of logistic models with time delays) was retained although obscured, with troughs somewhat elevated and peaks truncated (Fig. 7B) compared to the deterministic model. In others, population cycles were barely discernible (Fig. 7C). On occasion, the density-dependent time-delay and the immediate snow effect worked in tandem to produce rapid declines from high density. An interesting and general feature of Model 4 was that the chance of severely overshooting K was reduced appreciably with moderate to high environmental variability (e.g., Fig. 7B,C).

Conclusions

Our results imply two effects of snow caribou demography (Fig. 8). First, a density-independent effect, such that K with snow is less than K without snow. Second, a stabilising effect of snow as a consequence of the non-linear relationship between snow cover and r (Fig. 2), and the increase in variance of the snow cover effect with N (Fig. 4). This second influence may arise because caribou themselves affect the properties of snow cover, an interaction that may further depress population growth at high densities, in addition to any density-dependent resource limitations (Skogland 1985, 1986). Our Model 3, for example, infers no significant reduction in forage biomass *per se*, only in reduced access to forage resources in winter due to snow disturbance by caribou. In essence, this implies that K for caribou populations is not

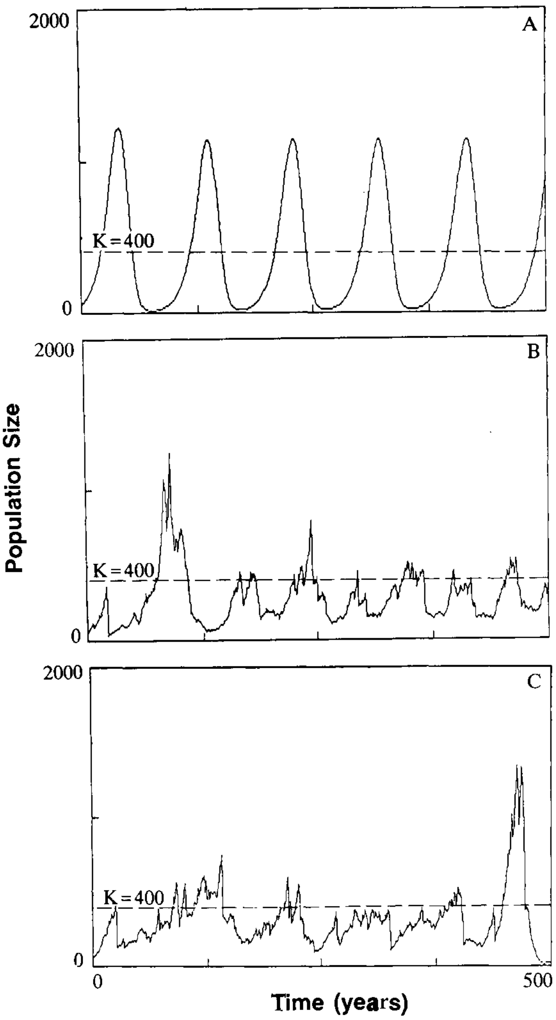

Figure 7. Typical population trajectories for (A) deterministic logistic growth and 20-year time delay (Messier *et al.* 1988), and (B,C) logistic growth with 20-year time delay and stochastic effect as dictated by Model 3B. The carrying capacity *(K)* without snow was set at 400 caribou in all cases.

static, but fluctuates on a year-to-year basis and with greater amplitudes at high caribou densities.

The combination of stochasticity, logistic growth, and time-delay (Model 4) suggests practical difficulties involved with attempts to unmask the factors regulating or limiting caribou populations. Similarly, Hassell (1985) remarked on such stochastic obstacles in the use of *k*-factor analysis of the mechanisms of population regulation in invertebrates. Nontheless, environmental noise remains the essence of the demography of numerous natural populations (Strong 1986). We believe that a better theoretical and empirical understanding of these influences remains integral to the management of *Rangifer.*

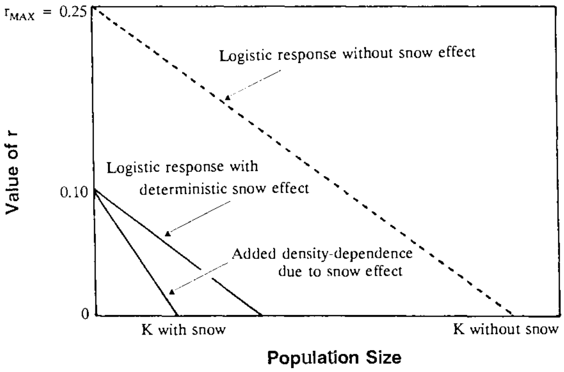

Figure 8. Hypothesised effects of snow on the rate of increase of caribou populations. (See text for explanation).

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Analysis of the standing age distribution and age-specific recruitment rate of the George River and Beverly barren-ground caribou populations.

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Abstract: The primary advantage of the standing age distribution of a population is that it can be sampled. Analysis of the age frequencies for estimates of survival rates and determinations of population status by life table construction depend heavily on assumption that require additional data to evaluate. The analysis of age structures for the George River (Messier *et al.* 1988) and Beverly (Thomas and Barry 1990a,b) caribou herd was reviewed. An alternativ method of estimating age specific survival rates was explored. The dependence of the life tables produced by the analysis of Messier *et al.* (1988) and Thomas and Barry (1990a, b) on tenuous and untestable assumptions regarding population growth rate over the life span of the oldest animals, stability of the standing age distribution, and constancy of life table parameters was emphasized. Although the life tables produced by Messier *et al.* (1988) for the George River herd and Thomas and Barry (1990a,b) for the Beverly herd are probably the best available for barren-ground caribou, they should be used with caution, particularly for management decisions.

Key words: age distribution, caribou, life table, mortality, *Rangifer*, recruitment, population dynamics.

Rangifer, Special Issue No. 7: 60—66

Introduction

The distribution of animals by age class (Standing Age Distribution) is one of the most common types of data available from harvested wildlife. The standing age distribution may be from a population that is stationary (i.e., neither increasing or declining), increasing, or declining. The standing age distribution may be stable (which occurs when the rates of recruitment and death have remained unchanged for a sufficient period) or unstable. For a given life table (i.e., a given set of age specific rates of recruitment and death) a single stable age distribution is defined.

Life tables are usually given for females only. Age specific recruitment (m_x) is only the number of females of age 0 produced per female of age x counted at the time of census. The time of census is not critical to defining the life table, however the time of census must be the same for the estimate of survival rate. The stable standing age distribution is defined for that time of census only. These rules are required to maintain an internally consistent life table.

The recruitment schedule and standing age distribution can be estimated from field data that is easily obtained. When the standing age distribution is both stationary and stable, the age specific annual survival rates can be estimated directly as the geometric mean rate of decline for age constant survival. Age specific survival (p_x) for the stable and stationary case is just N_{x+1}/N_x. When the population is stable, but increasing or declining, the estimate of survival rate must be corrected by the rate of population growth (λ):

$$p_x = \frac{N_{x+1}}{N_x x \lambda}$$

If the survival rate is known from cohort estimates (eg., radio telemetry) the standing age distribution may be compared to the expected stable age distribution calculated from the survival and recruitment schedules. The population growth rate at stable age distribution, and the population growth rate from the observed standing age distribution may be calculated. If the population growth rate is known from census estimates, and the population growth rate has remained constant, the age specific survival schedule may be calculated.

Caughley (1977) notes the futility of recalculating the population growth rate from the recruitment and «corrected» survival schedule. No matter what the recruitment schedule, and even if the standing age distribution is *not* stable, the assumed population growth rate correction will be recovered. Analysis of the standing age distribution for estimates of survival rates requires that the age distribution is stable, (i.e., the population growth rate known from census has been constant for the period of time specified by the maximum age).

The age distributions described in Messier *et al.* (1988) and Thomas and Barry (1990a,b) have been used to develop life tables for the George River and Beverly caribou herds. The resulting life tables depend heavily on untested assumptions regarding the stability of age distributions, and the constancy and value of the populations growth rate.

Methods

The terminology used is taken from Caughley (1977) and Taylor and Carley (1988). At stable age distribution the relationship between the recruitment schedule (m_x), the survivorship schedule (l_x), and population growth rate (λ) is given by the discrete form of the life table equation (Cole 1954):

$$1 = \sum_{x=0}^{\omega} l_x x m_x x \lambda^{-x} \qquad (2)$$

The relationship of the survivorship schedule to the survival rate schedule is:

$$l_{x+1} = \prod_{l=0}^{l=x} p_x \qquad (3)$$

where l_0 is defined as 0. The relationship of the survivorshp schedule (l_x) to the standing age distribution (S_x) is:

$$l_x = S_x x \lambda^{-x} \qquad (4)$$

where:

$$S_x = \frac{N_x}{N_0} \qquad (5)$$

Rewriting equation 2 using the relationship in equation 4 yields:

$$1 = \sum_{x=0}^{\omega} S_x x m_x x \lambda^x x \lambda^{-x} \qquad (6)$$

which reduces to:

$$1 = \sum_{x=0}^{\omega} S_x x m_x \qquad (7)$$

Cauchley (1977) warns against analysis for standing age distributions that begin with the assumption that they are stable. Using the definitions of S_x and m_x, equation 7 may be rewritten as:

$$\begin{aligned} 1 &= \sum_{x=0}^{\omega} \left(\frac{N_x}{N_0}\right) x \left(\frac{N_{0,x}}{N_x}\right) \\ &= \sum_{x=0}^{\omega} \frac{N_{0,x}}{N_0} \end{aligned} \qquad (8)$$

where $N_{0,x}$ is the number of age 0 females produced by females of age x. Equation 7 will always be true for any age distribution and any m_x schedule, stable or unstable, biased or unbiased.

The relationship in equation 4 is true only for stable age distributions. However, any age distribution (stable or unstable, biased or unbiased) can be corrected by some assumed population growth rate. Substitution for S_x from equation 4 in equation 7 gives equation 2, the life table equation. In other words the l_x schedule that results from the «correction» will, by definition, return the assumed population growth rate and initial standing age distribution as the stable age life table result (Caughley, 1977). This tautology does not test the stable age assumption or the accuracy of the «correction» term (λ).

The relationship between the standing age distribution (S_x) and age specific survival rate (p_x) can be developed from equations 3 and 4:

$$S_x = \prod_{l=0}^{x-1} \frac{p_l}{\lambda} \qquad (9)$$

The value of Φ for the mature adult age strata is best determined by the Chapman-Robson truncated method (Chapman and Robson, 1960) when survival rates are age constant:

$$\Phi = \frac{N_{x+1}}{N_x} = \frac{p_x}{\lambda} \qquad (10)$$

Table 1. The life table for the George River caribou herd as developed by Messier *et al.* (1988).

Age	Frequency	Recruitment rate	Standing age distribution	Corrected ($\lambda = 1.117$)	Smoothed		
(x)	(N_x)	(m_x)	(S_x)	$N_x \bullet \lambda^x$	N_x	p_x	$S_x \bullet m_x$
0	236.1	0	1.0	236.1	236.1	0.714	0
1	138	0	.585	154.0	168.5	0.99	0
2	156	0.06	.661	194.4	167.0	0.98	0.0397
3	113	0.35	.478	157.2	163.0	0.96	0.1673
4	94	0.40	.398	145.9	156.6	0.94	0.1592
5	83	0.40	.352	143.9	147.9	0.93	0.1408
6	65	0.40	.275	125.8	137.3	0.91	0.1100
7	63	0.40	.267	136.1	125.0	0.89	0.1068
8	57	0.40	.242	137.4	111.4	0.87	0.0986
9	40	0.40	.169	107.6	96.6	0.84	0.0676
10	24	0.40	.107	72.1	81.2	0.81	0.0428
11	18	0.40	.076	60.4	65.4	0.76	0.0030
12	12	0.40	.051	44.9	49.5	0.69	0.204
13	7	0.40	.030	29.2	33.9	0.56	0.0120
14	1	0.40	.004	4.7	18.8	0.24	0.0016
15	4	0.40	.017	20.8	4.4	0.10	0.0680
				$\lambda = 1.117$			$\sum = 1.0$

Results

The standing age distributions reported by Messier *et al.* (1988) and Thomas and Barry (1990a) were reported as stable age distributions with assumed population growth rates of 1.117 for the George River Herd and 1.0 for the Beverly Herd. Messier *et al.* (1988) used recruitment rates from other sources to develop a life table for the George River herd. The «natality» rates reported by Thomas and Barry (1990b) for the Beverly herd may be taken as recruitment rates by considering age 0 to be unborn calves.

The life Table for the George River herd is given in Table 1, and the life table for the Beverly herd is given in table 2. As described above, life tables developed in this manner always return the assumed population growth rate as the stable age growth rate, and the observed standing age distribution as the stable age distribution. The survival rate estimates are based on the assumption that the population growth rate has been constant over the time span embodied by the age distribution, that survival rates have not varied systematically, and that the age distribution was sampled without bias (Messier *et al.* 1988; Thomas and Barry 1990a,b). A George River life table was developed assuming the population growth rate was 1.0 to illustrate Caughley's (1977) tautology of age distribution analysis (Table 3). Similarly, recruitment rates for the George River herd can be arbitrarily doubled and the «corrected» life table will still return the correction as the stable age population growth rate (Table 4).

Both Messier *et al.* (1988) and Thomas and Barry (1990a) used a linear regression to fit the quadratic equation to the age distribution data. Linear alternatives that assume constant age specific survival rates within a given age stratum (Figures 1 and 2) gave an equally good fit to the data. The linear approach suggested 2 age strata of caribou could be identified: «mature» (age 2-10) and «senescent» (age 11-16). The Chapman-Robson estimates for the 2 strata are given for both George River and Beverly herds (Table 5). The recruitment rates for senescent age classes did not appear to decline (Thomas and Barry, 1990b).

Discussion

The standing age distribution is a history of the population dynamics over the period embodied by the number of age categories. It is information rich and easily measured. Age specific recruitment is also relatively straight-forward to measure. However, the information contained in the standing age distribution is not accessible without other information. As seen from the examples: stable and unstable; and biased and unbiased age distribution all give estimates of survival rates that are indiscernible.

Constancy checks are possible when additional information is available. Caughley (1977) argues that survival and recruitment rates are age constant for adult females of most harvested species. The caribou age distribution data suggests that the survival rates of senescent adult females are about 74% of mature animals. When survival rates of age strata are age constant, the Chapman-Robson Φ (p_x/λ), estimated from a stable age distribution, gives the relationship between survival rates and population growht rate. When the survival rate of mature ($x > a$) females is age constant (Caughley 1977) equation 8 may be rewritten in a manner that is useful for testing the stable age assumption from available field data:

a = age for first reproduction,
w = final age class
$\Phi = p_x/\lambda$ (constant for mature adults);

$$1 = S_a x m_a + \sum_{x=a}^{\omega} S_a x \, \Phi^{x-a} x m_x \qquad (11)$$

A measure of devation from stable age distribution (D) may be defined as:

$$D = 1 - S_a x m_a + \sum_{x=a+1}^{\omega} S_a x \, \Phi^{x-a} x m_x \qquad (12)$$

This devation from Stable Age Distribution (D) depends on the number of age 0 (N_0) and the number of N_x for $x \geq a$ (i.e., S_x); and the number of N_0 per N_x for $x \geq a$ (i.e., m_x). Age specific juvenile survival is not an issue. An estimate of the variance of D may be calculated using Monte Carlo methods from the variance of Φ calculated from the Chapman-Robson procedure, and the variance of m_x (pooled age classes or age specific as required).

The deviation from stable age distribution defined by equation 11 examines the consistency of the standing age distribution with the known underlying life history. A deviation from stable age distribution may be interpreted by examining the fit of the Chapman-Robson Φ to the adult strata of the standing age distribution (see Figures 1 and 2). If the residuals are symmetrical, the deviation is probably due to an incompatibilitiy between the recruitment schedule and the standing age distribution. Asymmetrical residuals indicate that survival rates may not be age constant, survival rates may

Table 2. The life table for the Beverly caribou herd as developed by Thomas and Barry (1990a,b).

Age (x)	Frequency (N_x)	Recruitment rate (m_x)	Standing age distribution (S_x)	Corrected ($\lambda = 1.007$) $N_x \cdot \lambda^x$	Smoothed N_x	p_x	$S_x \cdot m_x$
0	305	0	1.0	305	305	0.478	0
1	146	0	0.478	146	145.9	0.929	0
2	136	0.06	0.444	136	135.5	0.896	0.027
3	120	0.3585	0.398	120	121.4	0.889	0.142
4	109	0.4075	0.354	109	107.9	0.881	0.143
5	83	0.4275	0.312	83	95.2	0.872	0.132
6	101	0.4375	0.272	101	83.0	0.864	0.118
7	70	0.4375	0.235	70	71.6	0.847	0.102
8	59	0.4375	0.199	59	60.8	0.834	0.086
9	52	0.4375	0.166	52	50.6	0.813	0.072
10	45	0.4375	0.135	45	41.2	0.785	0.058
11	21	0.4375	0.106	21	32.3	0.745	0.045
12	31	0.4545	0.079	31	24.2	0.696	0.035
13	12	0.4545	0.055	12	16.7	0.582	0.024
14	9	0.4545	0.032	9	9.8	0.375	0.014
15	2	0.4545	0.012	2	3.7	0.000	0.005
				$\lambda = 1.002$			$\Sigma = 1.0$

Table 3. A life table for the George River caribou herd based on the same information as given in Messier *et al.* (1988) but corrected for an assumed population growth rate of 1.00.

Age (x)	Frequency (N_x)	Recruitment rate (m_x)	Standing age distribution (S_x)	Corrected ($\lambda = 1.001$) $N_x \cdot \lambda^x$	Smoothed N_x	p_x	$S_x \cdot m_x$
0	236.1	0	1.0	236.1	236.1	0.6567	0
1	138	0	.585	138	155.0	0.8622	0
2	156	0.06	.661	156	133.7	0.8584	0.0397
3	113	0.35	.478	113	114.8	0.8536	0.1673
4	94	0.40	.398	94	97.9	0.8474	0.1592
5	83	0.40	.352	83	83.0	0.8397	0.1408
6	65	0.40	.275	65	69.7	0.8298	0.1100
7	63	0.40	.267	63	57.8	0.8168	0.1068
8	57	0.40	.242	57	47.2	0.7995	0.0968
9	40	0.40	.169	40	37.8	0.7757	0.0676
10	24	0.40	.107	24	29.3	0.7406	0.0428
11	18	0.40	.076	18	21.7	0.6868	0.0030
12	12	0.40	.051	12	14.9	0.5914	0.0204
13	7	0.40	.030	7	8.8	0.3807	0.0120
14	1	0.40	.004	1	3.4	0.2310	0.0016
15	4	0.40	.017	4	0.8	0.0	0.0680
				$\lambda = 1.001$			$\sum = 1.0$

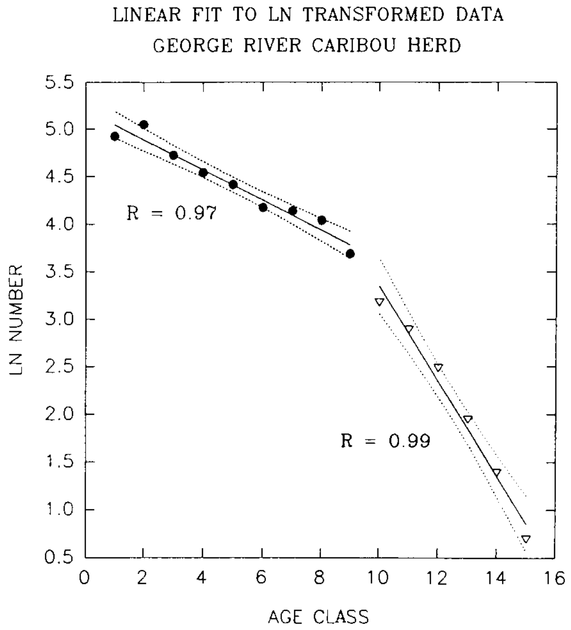

Fig. 1. The standing age distribution of the George River caribou herd (Messier *et al.* 1988) may be divided into «mature» (age 2-9) and senescent (age 10-15) age strata that have age constant rates of decline (Φ).

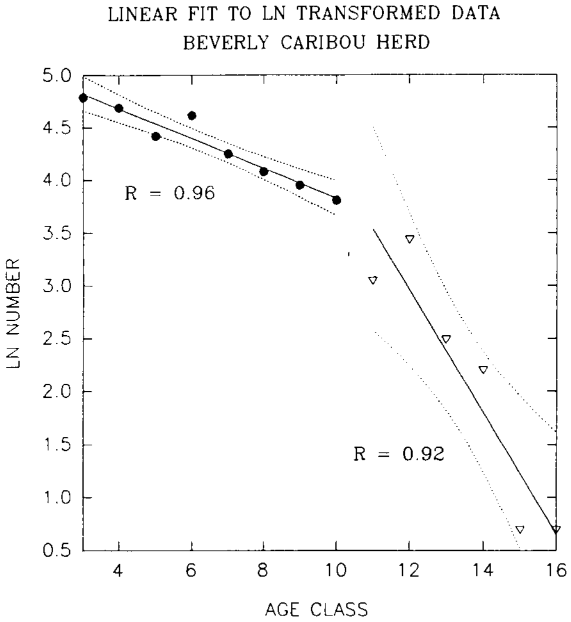

Fig. 2. The standing age distribution of the Beverly caribou herd (Thomas and Barry 1990a) may be divided into «mature» (age 2-10) and senescent (age 11-15) age strata that have age constant rates of decline (Φ).

have increased or decline, or population growth rate may have increased or declined.

The devation from stable age distribution (D) calculated from the George River herd using mature (0.87) and senescent (0.64) values of Φ was -0.401 (SE = 0.100). The deviation from stable age distribution calculated for the Beverly herd using mature (0.86) and senescent (0.63) values of Φ was 0.251 (SE = 0.074). These deviations suggest some caution in interpreting the age distributions of these herds as stable, but do not demonstrate that the age distributions are not stable. A «D» value that is significantly different from 0 signifies inconsistent assumptions, but does not identify which assumptions are incorrect. As stated above, if the Φ values are calculated as age specific, D will equal zero. Using flexible equations (such as the quadratic) to fit observed age distributions offers limited opportunity to examine the underlying assumptions involved in analysis of standing age distributions.

An inconsistency in the life table developed by Thomas and Barry (1990a) was noted. Barry and Thomas (1990a) give survival rate estimates based on the assumption that the population growth rate is 1.0 (i.e., no correction term). They suggest the mortality rate for age 0 is 37% (Thomas and Barry 1990a, page 183), and the mortality rate of age class 1 is 10% (Thomas and Barry 1990a, page 179). This gives a survival rate of 0.567 for age 0 to age 2, the first age class they feel is reliably represented. However, the fecundity data given in Thomas and Barry (1990b) indicates that N_0 = 305 and N_2 = 136. This indicates a survival rate of 0.446 assuming the stable age λ = 1.0. This discrepancy is easily corrected by just accepting the age distribution estimate. A defensible argument for that approach would be that intra-uterine mortality was neglected in the lower calf mortality estimate.

Conclusion

Analysis of standing age distributions is an enigma. I appears that unless there is considerable additional information about population growth rate and age specific rates of survival, analysis of standing age distributions only returns the initial assumptions. Both Messier *et al.* (1988) and Thomas and Barry (1990a,b) were well aware of the assumptions they made in examining the George River and Beverly standing age distributions. It did not appear that the data were sufficient to resolve whether survival rates were age specific or age constant for either age distribution. The data were also insufficient to determine whether the age distributions were unbiased or stable. Suspected changes in the population dynamics of both herds were mentioned by Messier *et al.* (1988) and Thomas and Barry (1990a,b) which would have caused deviation from stable age configuration.

Table 4. An example taken from Messier *et al.* (1988) to illustrate that the sum of the standing age frequency (S_x) times the recruitment rate (m_x) does not depend on the values of m_x (i.e., it is always 1.0).

Age (x)	Frequency (N_x)	Recruitment rate (m_x)	Standing age distribution (S_x)	$S_x \cdot m_x$
0	472.2	0	1.0	0
1	138	0	0.292	0
2	156	0.12	0.330	0.0397
3	113	0.70	0.239	0.1673
4	94	0.80	0.199	0.1592
5	83	0.80	0.176	0.1408
6	65	0.80	0.138	0.1100
7	63	0.80	0.133	0.1068
8	57	0.80	0.121	0.0968
9	40	0.80	0.085	0.0676
10	24	0.80	0.051	0.0428
11	18	0.80	0.038	0.0030
12	12	0.80	0.025	0.0204
13	7	0.80	0.015	0.0120
14	1	0.80	0.002	0.0016
15	4	0.80	0.008	0.0680
Any m_x schedule → stable age distribution				$\sum = 1.0$

The life tables developed for the George River and Beverly herd were consistent with the available data and the assumptions given. The recruitment rates given by Thomas and Barry (1990b) were measurements rather than interpretations. However, the other life table parameters for both the George River and Beverly herds are most correctly understood as hypotheses which currently depend on un-testable assumptions.

Life tables provide powerful tools for wildlife managers. However, it appears that the useful-

Table 5. The Chapman-Robson (Chapman and Robson 1960) truncated values of Φ for «mature» (age 2-10 and 2-9) and «senescent» (age 11-15 and 10-15) age strata are given for the Beverly (Thomas and Barry 1990a) and Georg River (Messier *et al.* 1988) caribou respectively.

Beverly herd

Age Strata	C-R PHI (Φ)	SE of Φ
Mature (age 2-10)	0.87	0.02
Senescent (age 11-15)	0.64	0.06

George River herd

Aga Strata	C-R PHI (Φ)	SE of Φ
Mature (age 2-9)	0.86	0.02
Senescent (age 10-15)	0.64	0.06

ness of standing age distributions is limited unless there is precise and accurate population census data to accompany it. The ideal data set would include cohort estimates of age specific survival rates, age specific recruitment rates, and an independent census to confirm the population dynamics suggested by the resulting life table. Simulation studies might improve qualitative understanding of the value and dangers of simplifying assumptions to life table analysis of caribou.

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Printed from manuscript after editorial review.

Joint management inaction - George River caribou herd

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Keywords: George River caribou herd, Labrador Inuit Association, explotation of land

Rangifer, Special Issue No. 7: 67—72

Introduction

This paper is not a scientific presentation of data on the George River caribou herd. Nor is it a scientific interpretation of the status of the herd. This paper is about a major caribou herd that may be in trouble and the belief of the Labrador Inuit Association (LIA) that the biggest current threat to the health of the herd may be the management policies of governments.

Our experience and knowledge of the herd combined with the data collected by biologists over the years suggest to us that the George River herd may be at risk. We are not interested in getting involved in the techincal and sometimes academic arguments about census techniques, confidence levels and theories of population dynamics. We are primarily concerned about the information base that is used by government managers and the politics that continue to influence management policies.

The Labrador Inuit are watching with real concern as the governments of Quebec and Newfoundland deny some of the indicators suggesting the George River herd may be in trouble and proceed to manage it in isolation from its biophysical realities and in defiance of principles of conservation.

In this paper we will highlight what LIA considers to be the essence of what Labrador Inuit know about the herd as it should affect management policies for the George River herd. We will also point out what we believe to be some of the major external threats to the herd and focus on the absence of a joint management regime and the complete lack of political will on the part of Quebec and Newfoundland to work co-operatively.

The George River caribou herd

The George River caribou herd is most likely the largest caribou herd in the world. These caribou, generally considered to be barren ground caribou, range throughout the entire Labrador/-Ungava Peninsula which is split into the two political jurisdictions of Quebec and Newfoundland.

The caribou spend most of the winter spread across the barrens of Northern Quebec as far west and north as the coast of Hudson' s Bay. Migration eastward begins when the females start to move in early March if conditions permit. Females reach the main calving grounds in the upland tundra area in the height of land between Quebec and Labrador at the end of May or early June. Throughout the summer the animals disperse and are found along the north coast of Labrador and north to Ungava Bay. In late summer and early fall the caribou head west again for their winter range.

One of the most impressive things about the annual migration of the George River caribou herd is the distance that is covered. A satellite collar deployed on an animal captured near Hebron on the coast of Labrador can later put out a signal from the Caniapiscau River. The herd lately has been shifting and while the general east/west migration pattern is constant we see changes in migration patterns and behaviour. In 1990 the caribou did not come into Labrador until mid-May. This was the first time this had happend in living memory.

There are a number of aboriginal peoples living in the Labrador/Ungava Peninsula whose culture, economy and society are tied to the George River herd. In Labrador the herd is hunted by the Labrador Inuit who live along the coast of Labrador and the Naskapi/Montagnais Innu. Labrador Inuit will sometimes travel west of the George River in search of caribou for their families.

In Quebec the Inuit, Naskapi and Cree all traditionally and currently hunt the George River caribou. In addition to the Quebec aboriginal users there is a very significant sports hunt. The land claims of the Cree and the Inuit of Quebec have been settled and their rights are set out in the James Bay and Northern Quebec Agreement (JBNQA). The claims of the Naskapi of Schefferville have also been settled and their rights are set out in the North Eastern Quebec Agreement (NEQA).

Under the JBNQA and the NEQA the rights of the Quebec Inuti, Cree and Naskapis to take levels of caribou sufficient to meet their needs are guaranteed. These agreements also guarantee a management body known as the James Bay Hunting Trapping Fishing Coordinating Committee. While this is an advisor committee to the Minister Responsible for Wildlife it is a cooperative management arrangement with representation from all three arboriginal parties, the Quebec government and the government of Canada. A specific provision in the agreements allows the Coordinating Committee to establish the upper limit of kill for caribou subject to the principle of conservation which is defined in the JBNQA as follows:

> «Conservation means the pursuit for the optimum natural productivity of all living resources and the protection of the ecological systems of the territory so as to protect endangered species and to ensure primarily the continuance of the traditional pursuits of the Native people, and secondarily the satisfaction of the needs of non-Native people for sport hunting and fishing».

The sports hunt kill in Quebec takes almost as much as the subsistence hunt. Recent figures put the Quebec kill by sports hunters at 9,000 animals and the subsistence kill at 10,000 animals. It is a very different situation on the Labrador side. There are no land claims agreements with the Inuit or the Innu. The LIA has only just started negotiations towards settling its outstanding claims. The Innu are not yet at the table. There are no formal arrangements with Newfoundland that provide any guarantee or form of protection for priority allocations for aboriginal people in Labrador. All that LIA has is a reassurance from a Minister responsible for Wildlife in a previous government that priority would be given first to the subsistence hunt, second to the commercial hunt, and last to the sports hunt. Caribou numbers have not gone low enough to test that assurance.

There is no management arrangement in Newfoundland that provides for co-operation with aboriginal users. There is no effort on the part of the Newfoundland government to solicit the participation of the Labrador Inuit or Innu with respect to management decisions.

The LIA operates a commercial caribou hunt through its economic arm - the Labrador Inuit Development Corporation taking an average of about 500 animals per year so far.

What we know about the herd

We know that the George River herd is large and is likely the largest caribou herd in the world. We know that the herd is no longer increasing. We suspect that it has been decreasing at a rate of about 7-9% per year for the past few years. Evidence from the past few years also suggest that the caribou coming off the summer range are in very poor nutritional state and some animals have started to death.

The main calving grounds used by the George River animals have been used consistently over the past 20-30 years and preliminary work indicates that the calving grounds are almost bare of forage. There is some intermingling of descrete herds with the George River herd especially where the Leaf River and George River caribou share the same winter and rutting ranges. The range of the George River herd in the winter sometimes extends to include range that is used by more southern woodland herds.

What we do not know about the George River herd?

We do not have a population estimate of the George River herd that is accepted equally by government managers, government biologists and arboriginal users. Population estimates for the George River herd now range from 150,000 to 680,000. The governments of Newfoundland and Quebec appear to be basing their management policies on the high estimate of 680,000. Biologists for Quebec and Labrador believe the count is lower.

We are seeing changes in migration routes and patterns of the George River herd but we don't know what precipitates them. There are som theories and speculation only. We know that certain environmental factors especially ice and snow in the winter and insect harassment in the summer can influence cariobu behaviour and migration. However we don't really understand what factors are at work. For instance we do not know why the caribou 'did not show up' in Labrador in 1990. We do not know the impact of wolf predation on the caribou nor do vi know very much about the quantity , quality and nutritional levels of the vegetation throughout the George River herd's range.

What we have just outlined is a simplistic and incomplete overview of what we know and don't know about the herd for management purposes. Obviously such an overview is not intended to undermine all of the work done by scientists and wildlife managers. Rather it is intended to put things into perspective.

Some of the very basic issues that are essential to responsible wildlife management are unknown. We know the herd is declining but we can't even agree on its size. We know animals are starving at a time when they should be building up their fat and nutritional reserves. We think there may be a problem with the carrying capacity of the range but we don't know.

We are not naive enough to expect to have answers to all these unknowns but we do expect that managment policies operating within these parameters should be conservative and sensitive to the number of unknown variables. Management should also be sensitive to, and take into account, the external factors that may also pose a threat to the herd.

Threats to the herd

The Department of National Defence (DND) and various North Atlantic Treaty Organization countries have been practising low level flying in Labrador for eleven years. Until 1990 there was no monitoring of the effects of low level flying on caribou or on habitat. The exception was a two year study done by Dr. Fred Harrington on the effects of low level flying on the behaviour of George River caribou. Because of time and funding constraints the study was inconclusive. Low level flying is practised from mid April to the end of October and a significant portion of the George River caribou range falls inside the low level flying zone. No long term monitoring studies have been initiated, no appropriate baseline studies have been done. With eleven consecutive years of low level flying we are unable to answer any questions about the effect of such activities on the health and behaviour of the George River caribou herd or on its habitat.

Current plans of Hydro Quebec involving the La Grande and the Great Whale Rivers in western Quebec potentially threaten important habitat used by the George River caribou. Both river systems, and particularly the Great Whale in the area of Lac Bienville, have been documented as having become a prime and/or preferred winter range for a portion of the George River caribou herd. Caribou collared[1] in the Torngat Mountains, north of Nain, in the late summer subsequently crossed the Labrador Peninsula during the autumn to over-winter in the Great Whale River drainage. It is very difficult for us in Labrador to get any information on what is actually happening in Quebec. The initiative is being addressed as a project with no trans-boundary impacts and there is no pressure coming from outside Quebec to address any trans-boundary impacts. It is extremely unrealistic to expect that James Bay II will not impact on the George River herd but how and to what degree we do not know. Many efforts to predict impacts will be reliable only to the degree to which they incorporate the current situation of the George River herd.

The governments of both Newfoundland and Quebec are relying on the high population estimate for the George River herd. Each government establishes kills independent of the other. Because the herd is large it is considered to be «under-harvested».

For the past few years Quebec has been working very hard to push for a commercial kill which is currently not allowed under the JBNQA or NEQA. Originally the commercial quota was for 40,000 now it is in the range of 15,000.

Joint management inaction

LIA believes that the single biggest threat to the health of the George River herd is the current approach to management by the governments of Newfoundland and Quebec. Dialogue between Newfoundland and Quebec has never been great and it is virtually non-existent in terms of management responsibilities for George River caribou. Each government manages the herd as if it is within its sole jurisdiction and does not migrate outside provincial boundaries.

In the early 1980's LIA met with Quebec and Newfoundland officials to try to initiate discussions that would lead to some form of joint management arrangement for the George River herd. We were not successful. The political agendas of the two governments are such that there is no room to talk about joint management. Long standing disputes between Newfoundland and Quebec over the sale of Churchill Falls power and the Quebec/Labrador boundary leave no room for, or political will to discuss joint management of a shared resource, particularly when each sees that resource as being under-harvested. LIA also met with the aboriginal groups in northern Quebec to see if we could generate the initiation at that level. We failed there too. Apart from some interest shown by Makivik (which represents the Northern Quebec Inuit) there was no follow through. In 1984 when LIA was negotiating with Quebec and the Inuit Cree and Naskapi signatories to the JBNQA and the NEQA for rights to hunt in Quebec we tried to make joint management an issue. We failed again. We discovered that it was not an appropriate forum because we did not have all the necessary participants. We were missing the Newfoundland government and the Labrador Innu.

LIA also spent considerable effort trying to get Canada involved at least as a facilitator for negotiations between Quebec and Newfoundland. But Canada has its own political agenda and at the time was not prepared to be seen as intervening in any way in the political squabbles or the provincial jurisdictions for the two parties. And so we have had to stand back and watch as a resource as vital as the George River caribou herd pays the price for bitter, positional political agendas. This then, has become the biggest threat to the George River herd.

It is very alarming to watch governments default on their management responsibilities the way Newfoundland and Quebec continue to do. Each government jealously guards its jurisdiction over wildlife and rabidly defends what it believes to be its jurisdictional territory. But just look at how they interpret their management responsibilities. First, as we have said, they manage the herd as if it stays within provincial boundaries. Not only does that deny the reality of herd dynamics, it also requires unnecessary duplication of cost and effort for certain things like surveys and radio collaring. Despite warnings from aboriginal users and from some of its own biologists Quebec and Newfoundland both choose to accept the highest population estimate for the herd and continue to push for larger kills. Questions about the census, about the methods used to establish the population levels and warnings about a decline in the population should generate a management approach that is cautious and errs on the low side. Quebec and Newfoundland are reckless about establishing levels and allocations of kills from the herd because they believe it is large enough that it can absorb whatever they permit.

At a time when the population count is uncertain and the herd in a state of decline management policies should be especially sensitive to additional external threats that may add to the stress of an already stressed herd. Yet neither government has taken any lead in trying to regulate, or at least monitor the effect of low level flying on the George River herd. In fact Newfoundland is a strong advocate for the military presence in Goose Bay. Its political agenda has little tolerance for actions that would place a burden on DND's flying activities.

The Federal Environmental Assessment and Review Panel established in 1986 to assess the environmental impacts of low level flying has stalled. The Environmental Impact Statement prepared by DND was declared deficient by the Panel in May 1990 and we are still waiting to hear what happens next. Since the Review Panel was established we are now entering the sixth season of low level flying. We have been a lone voice protesting this. Finally DND agreed to negotiate a Memoradum of Understanding with LIA which among other things planned a monitoring program to be carried out by LIA and funded by DND.

When Newfoundland discovered that DND planned to fund LIA to put satellite collars on caribou they intervened in our discussion and made it clear LIA had no jurisdiction, or right, to put collars on caribou. Newfoundland rejected a proposal that would have seen LIA contract the Newfoundland wildlife division to put on the collars. Newfoundland protested so loudly that LIA forfeited that part of the plans under the Memorandum of Understanding in order to save its other features. Newfoundland then stepped into the ring at the eleventh hour claiming an interest in establishing a monitoring plan for 1990. Newfoundland would have maintained its wall of silence on the issue if it had not perversely believed that in securing funding for satellite collars LIA was somehow threatening its jurisdiction.

Right to manage

We are becoming bitter about what we see happening and afraid of what the consequences will be. The question we ask ourselves is «by what rights does either Newfoundland or Quebec have jurisdiction over wildlife»? Surely jurisdiction for wildlife implies a role of stewardship. By vesting jurisdiction for wildlife in the Crown the intent is to ensure responsible stewardship of the resource for the citizens of the province or the county, as the case may be. LIA believes that defaulting on that responsibility should be a criminal offense. We watched while government mismanaged and ultimately decimated the northern cod stocks off our coast. We pay the consequences for this action. We go hungry and watch as a critical part of our future harvesting rights are wiped out. But what happens to the government managers and policy makers, to all of those people who, in exercising their powers violated the very responsibility that was vested in them? Nothing. Their jobs are secure, their futures are secure. They are simply not accountable. We don't mean accountable in the political or electoral sense. That may be enough in an industrial society that does no depend on renewable resources and that probably has the kind of population base that could make electoral accountability mean something. We mean legally accountable or legally liable with legally enforceable remedies.

The Labrador Inuit are an aboriginal people whose lives, culture and economy depend on access to healthy populations of wildlife. How can we be expected to respect government's claim to jurisdiction over wildlife when their political agendas override responsible management based on conservation? How would the system change if there was a way to make governments legally liable for the consequences of negligence in wildlife management policies? We are not lawyers but we strongly suggest to those people who are lawyers or who are interested in public policy and who care about the future of certain wildlife populations to go out and be creative and find a way that can make governments legally accountable for their actions. We believe this applies equally to Canada with respect to the George River caribou herd. We believe Canada has jurisdiction for transboundary migratory species and it too has stewardship responsibilities on behalf of the Canadian public. Canada can see what is happening to the George River herd and yet it will not intervene despite the obvious violations of the principles of sound management and conservation. These violations are, if nothing else, a breakdown in order and good government within the Country. Canada's silence on this issue also calls into question its commitment to the principles of environmental protection and wildlife management which form the basis of the newly announced Green Plan. It is also difficult to take seriously Canada's commitment to environmental protection on the international scene when it chooses to abdicate its responsibilities at home.

Conclusion and recommendations

LIA is discouraged and afraid of what governments may be doing to exacerbate and accelerate a decline in the health and numbers of the George River caribou herd. We have a major migrating herd that is becoming the victim of political divisions between Newfoundland and Quebec. There are other major herds in the country that involve more jurisdictions than just two provinces. The Beverly/Kaminuriak Joint Management Board has two provinces, a territorial government and federal government as well as the major aboriginal users all represented on it. The Porcupine Caribou Herd Management Board has two territorial governments, the federal government and Alaska as well as the major aboriginal users represented on it. These management boards are not without their problems but they are success stories in the field of co-operative management. They provide a means by which best efforts can be made to manage a wildlife population in a way that integrates wildlife and habitat, uses the best information available, optimizes research efforts and respects the principles and practices of conservation.

It is a tragedy that such a system cannot be established for the George River herd because there is no political will. It is especially tragic that the Quebec and Newfoundland governments choose to ignore the indications that we believe are signalling trouble. Governments can afford to operate in this manner because they are not legally liable for their actions. It is the aboriginal people who will pay the cost. LIA has given this situation much tought and we have come up with two possible courses of action:

1) Canada could commit to a financing and convening process to deal with conflict resolution and interest identification associated with the governments and the aboriginal users involved with the George River caribou herd in a way similar to that done by Don Snowden for the Beverly/Kaminuriak herd.

   The governments have failed to act responsibly as managers of the George River herd and they have helped to create a management crisis. LIA believes that the aboriginal users of the herd also have a duty to act as responsible managers and this duty exists independent of what governments may or may not do. It is time for the aboriginal users in Quebec and Labrador to act unilaterally and in the interests of the herd. The Inuvialuit in the western Arctic were able to negotiate with the Inupiat in Alaska a co-management agreement on polar bears. We should be able to do a similar thing with caribou.

2) Accordingly, LIA is prepared to consider taking initiatives to bring together the major aboriginal users of the herd for purposes of discussing a way of establishing a joint management agreement. LIA considers that the JBNQA could act as a vehicle in the interim through which the aboriginal users could give expression to an aboriginal joint management agreement. No such vehicles exist in Labrador.

Printed from manuscript after editorial review.

Wildlife Co-management defined: The Beverly and Kaminuriak Caribou Management Board

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Abstract: A comparison of indigenous and scientific forms of wildlife data gathering and conservation/management reveals similarities and differences. The two systems are needed to effectively manage wildlife in northern Canada, particularly migratory, trans-boundary species. The Beverly and Kaminuriak Caribou Management Board brought multi-jurisdictional caribou users and managers together to co-manage two large herds of caribou *(Rangifer tarandus groenlandicus)*. The advisory Board's principal duties and responsibilities are communication and to maintain the two herds at population levels that will meet user needs. Goals, objectives, and principles are set out in a management plan. Board activities are structured in 15 action plans under major categories of communication, supply of caribou, use of caribou, and habitat. Board successes are attributed to use of the plan to guide actions; to the Chairmen and vice-Chairmen; to the quality of founding members and their continuity; to effective vehicles of communication such as a newspaper, radio, video, and community meetings; to a spirit of cooperation; and to high caribou numbers because of high productivity combined with poor accessibility. Problem areas include technical limitations, members' decreasing powers and increasing turnover, inadequate communication of Board objectives and activities within the communities, and accountability. Future challenges include the management of caribou shortages, obtaining better herd data, and the need for more intensive management as user populations grow.

Keywords: caribou, caribou management board, conservation, management

Rangifer, Special Issue No. 7: 73—89

Introduction

Management of the great caribou herds that migrate between forests and tundra of the Canadian mainland and across political boundaries poses a great challenge. Traditional user groups include many different cultures of Inuit, Chipewyan, Cree, and Metis and a few white trappers with special hunting licenses in the Northwest Territories (NWT). These groups have unrestricted use of the caribou resource by treaty, aboriginal rights, special licences, and tradition. Southern forms of wildlife management had limited application. They are based to a large extent on regulating the kill by hunters. Regulations were foreign to users and their imposition unacceptable for several reasons. Enforcement of any rules was difficult to impossible.

A further serious problem was obtaining reliable scientific data on the herds. Costs were extremely high and difficult to justify unless management was possible. Data obtained in the late-1940s and 1950s indicated a serious decline in caribou numbers (Banfield 1954, Kelsall 1968). Inter-government committees were established to coordinate research and look for management solutions. Regulations on use of caribou, educational programs, and wolf poisoning were introduced to stem the decline in caribou numbers (Kelsall 1968). From 1967 through 1972, an attempt was made to fight fires on the winter range of the Beverly herd. After apparent recovery of caribou numbers in the 1960s and 1970s, a serious decline in the Kaminuriak herd was indicated by survey data in 1980. The native people disagreed with the survey data. In 1979-80, the Beverly herd wintered in northern Saskatchewan in areas accessible by road and 15,000-20,000 were killed. Native users were blamed for caribou declines. A confrontational atmosphere developed between users and wildlife biologists/managers.

In the late 1970s, it became obvious to government managers that the native people must be part of the solution to management of the Beverly and Kaminuriak herds of caribou. The first step was to get native users and government managers around the same table to discuss the problem and seek solutions. This led to the first co-management caribou board described herein.

How can co-management work best? First of all, native users must learn about scientific forms of management and biologists and managers must learn about native culture and attitudes towards wildlife. The scientific form of wildlife management was virtually unknown by native users of caribou. In the 1980s, papers began to appear on indigenous forms of conservation and management (Freeman 1985; Usher 1986, 1987; Feit 1988; Osherenko 1988; Riewe and Gamble 1988; Therrien 1988). The best aspects of both systems will be needed to improve northern wildlife management in general and caribou management in particular.

In this paper we compare scientific and indigenous forms of wildlife conservation/management; discuss co-management as an integrated approach; and examine one attempt at co-management: the Beverly and Kaminuriak Caribou Management Board (BKCMB). We then express personal views on current problem areas in the BKCMB and future challenges.

The scientific system of management

Scientific wildlife management was developed in the U.S.A. and southern Canada. The system is based om obtaining, storing, handling, manipulating, analyzing, and applying technical data. The goals of scientific wildlife management are to maintain wildlife populations at some level or between certain stated levels or densities. Populations must not be allowed to exceed the carrying capacity of their habitat or a rapid decline will occur. Often the management level is set to provide a certain level of sustained harvest. Historically, scientific management was aimed at providing a "harvest" surplus for hunters who are termed "consumptive users". As habitat was lost and populations declined, a greater emphasis was placed in just maintaining wildlife populations. Thus, conservation and endangered species programs are now part of some federal and provincial/territorial agencies. Provisions are also made for increasing proportions of non-consumptive users, e.g., bird watchers.

The major technical management tools are control or modification of hunting, predator control, and safeguarding or enhancing habitat. Hunting regulations are the major tool. Predator control is little used because of public opposition and, in some cases, the need to protect predators. The primary statistics used in management are estimates of population size or trend; population age and sex structure, particularly additions of young to the population; and deaths from hunting and natural causes.

The system has worked well in southern Canada and the U.S.A., including some large Indian reservations in the west. It has not worked well when applied to northern caribou herds. The main managerial problems in northern Canada are insufficient or unreliable data on the caribou herds, management tools are limited, habitat management is costly, and land management decisions consider other resources. The costs are enormous to obtain reliable data on herd distributions and numbers; recruitment (addition of 1-year-old caribou to the herds), natural mortality rate, and harvest level. Treaty rights guarantee hunting rights and equivalent rights are extended to non-treaty native people through General Hunting Licences (NWT) or by not enforcing laws and regulations.

Wolf control using poison and predator control officers was discontinued in the early 1960s because of its cost, it questionable effectiveness, and opposition to it from people outside northern Canada. A wolf bounty was discontinued in the early 1970s. Control of forest fires is exceedingly costly and of questionable effectiveness. Roads are developed in caribou range to access mineral resources and provide cheaper goods to northern settlements.

Indigenous forms of wildlife management

Native wildlife management termed "indigenous tradition", "traditional knowledge", "customary law", and "selv-management" (articles in Freeman and Carbyn 1988) have not been explained in any detail. One view, held or inferred by many northern zoologists, is that no historical evidence exists for active wildlife management of caribou in northern Canada (Banfield 1954; Kelsall 1968; Cowan 1969; Macpherson 1981; Theberge 1981; Thomas 1981; Miller 1982). The hunters and the caribou were in approximate balance before the introduction of modern equipment. Shortages of wildlife resulted in periodic starvation and management was by default. Native users were nomadic and shifted from one species to another as one became scarce, e.g., from caribou to sea mammals or from caribou to muskoxen or fish. The key point is whether there was active management or not. Was the kill of a species deliberately reduced when populations of that species were low? Aboriginal hunters and societies were most likely to survive if they took as many animals as possible when the opportunity arose. Meat was stored in various forms but if fresh meat was obtained some of the stored meat would not be used. Surplus meat was shared with other groups in the area that were less fortunate. Hunting restraints were unlikely for any sparse migratory population of animals in a hunting territory. The status of a hunter was proportional to his success at obtaining food. Thus, much behaviour relates more to survival than to conservation or management.

Many traditions concerning wildlife took the form of beliefs, myths, legends, and taboos that arise when favourable or unfavourable events were associated with a hunting incident or use of animals or, perhaps, in dreams. Myths and legends were handed down by oral tradition and no doubt changed through time. Our perceptions of people-caribou sytems therefore are based on recent history. The Dene and Inuit believed that caribou had souls that lived on after death and these must not be offended (Arnold 1989). This translated into respect for the animals. Spiritual links developed over time between the aboriginal hunters and their prey and these are particularly strong for caribou.

At the other extreme we occasionally hear almost mystical views of harmony between native hunters and their prey. Arguments for active management are articulated mostly by social scientists (Freeman 1985; Usher 1986, 1987; Feit 1988; Osherenko 1988; Riewe and Gamble 1988; Therrien 1988). In most cases, a few recent examples of harvest restraint of largely non-migratory species are extrapolated to other cultures with the assumption that active management was universal. Explanations of indigenous systems of wildlife management often include assumptions and general statements that are supported by few data. These assumptions are repeated by others until they are regarded as fact. Aboriginal societies had to develop conservation measures to survive but such practices should not be confused with active management. The problem may be semantics (language). There would be less confusion if "management" was replaced by "conservation" in many of the articles on indigenous societies-wildlife relationships. To a biologist, the term "overhunting" may mean that there are too many hunters for the number of caribou available for sustained harvest; to the hunter it may infer that he, as an individual, is taking too many caribou. Clear definitions of terms are needed to avoid misinterpretation and unnecessary conflict.

Pre-19th century, northern, indigenous societies must be admired for their ability to survive in a servere environment with an unstable resource base. We should not burden them with proof that they actively managed migratory wildlife resources. After Europeans arrived, the need for trade goods was so great that caribou were shot just for their hides as recently as 1960. What is lacking are explanations from native elders of where conservation or management occurred and how it was effected. With no written history, we must rely on oral accounts of human-wildlife relationships. No one disagrees that native users of wildlife are keen observers who detect changes in animal behaviour, health, and physical condition. Native hunters knew where caribou were likely to be at various times of the year but only within their territory or from conversations with neighbouring bands. Knowledge of caribou behaviour was a great asset in the hunting of caribou. For example, some caribou would be allowed to cross a river before some were killed. Otherwise all the caribou might use another crossing. The people learned through trial and error to avoid diseased parts of animals, although the major prey species were free of parasites obtained from eating meat. They were familiar with all the anatomical parts of animals. The use of all parts of caribou was a conservation and survival strategy. There was and is strong selection for the age and sex classes of caribou that are fattest during annual cycles of condition. Such selection favours human survival but not conservation because losses of adult females has the greatest impact on the growth of a population. Adult females are fattest over a greater proportion of the annual cycle than males. There are complications to any form of management where other groups hunted the same herd of caribou that ranged unpredictably over vast areas. Expanding native populations and modern support systems, hunting equipment, and transportation add new dimensions to equilibria between hunters and prey.

Traditions, beliefs, legends, folklore, and taboos change much more slowly than the introduced technology. Some beliefs influence indigenous peoples' attitude towards wildlife management: (1) that abundant animals will be provided by God, spirits, or other; (2) that animal populations are cyclic (e.g., Thomas 1981, Gunn *et al.* 1988); and (3) that animals can be offended by certain human actions. Thus, Chipewyan in northern Manitoba and Saskatchewan believe that caribou should not be handled or disturbed outside of hunting them (Bone *et al.* 1973, Müller-Wille 1974). If not disturbed, there will be plenty of caribou for all time. Hunting with rifles, snowmobiles, aircraft, and motorboats creates much more disturbance to the caribou than in the "old days" before Europeans arrived. Many wildlife populations have been eliminated through hunting with modern equipment. Caribou have not fully adapted to the rifle.

Differences between traditional and indigenous management

There are always interpretation problems and in particular when two or more languages are involved. The term "management" is interpreted differently by different groups. Management in indigenous systems usually means some form of harvest restraint or conservation. This is also the major tool of technical managers who use it to maintain sufficient numbers in a hunted population. In indigenous management there was, with a few recent exceptions, no accounting of numbers or achieving some balance between harvest and annual addition of young to populations.

Technical management may arbitrarily but functionally be divided into six steps: data collection, accumulation, analysis, interpretation, transfer; and management action. Gunn *et al.* (1988) divided the process into three steps. Hypothesis making and testing focuses the process particularly for theoretical questions. The six steps reveal similarities and differences in indigenous and scientific systems.

Data collection

Both methods of data collection are based on observations and the indigenous method is partly scientific. ("Science: knowledge; comprehension or understanding; knowledge coordinated, arranged, and systematized...", The New Webster Encyclopedic Dictionary). Scientists tend to formalize and standardize their quantitative observations. They tend to rely, excessively we might add, on proven methods of other scientists. This permits them to directly compare their data with those of the previous worker. Often the methods of study are changed to suit the new study. The best scientists devise new methods of collecting data and set a new standard. The scientist gathers quantitative and qualitative information from throughout the range of a caribou population, whereas the observations of indigenous hunters tends to be more localized and mostly qualitative. Nevertheless, the indigenous hunter may detect things and subtle differences that a scientist would overlook. Such observational data are termed "empirical" as opposed to theoretical.

Data accumulation

Indigenous "scientists" accumulate knowledge in their brain. Scientists accumulate observations in memory and in notebooks, on data forms, in computers, and summarize the observations in reports and publications of standard format. The accumulated written material becomes what is termed b aseline information on a subject to which new written observations are compared. Transmission is mostly by reports and publications, although there is transfer of information orally at meetings, workshops, and individually.

Data analysis

Another major difference in the two systems is that scientists are bound by certain conventions of how data are processed and presented. There are arbitrary limits on whether observations or data are real or are due to chance. They use statistics to make decisions about their observations. Generally, they attempt to collect large amounts of data to meet criteria for information adequacy. A high degree of variability occurs in biological data and there are additional errors associated with collecting it. Certain arbitrary levels of certainty (probability) are used to make decisions about data. For example, indigenous hunters would know that caribou were fat in a certain winter based on observations of carcass fat. The scientist reports that adult cows had 10 mm of back fat plus or minus 5 mm at a certain probability level, usually 95%. There are complicated statistical methodology to describe data, compare them with other data, and determine if relationships exist among variables (e.g., age, sex, and depth of back fat). These are termed quantitative (amount) analyses of data. Indigenous people describe things in more-general categories termed qualitative. There is a potential for scientists to dwell excessively on data analysis and manipulation and lose sight of some basic relationships. That is, scientists may rely too much on quantitative data and overlook obvious qualitative differences. For example, Geist (1991) argues that subspecies criteria for caribou should be based on qualitative differences in coat (pelage) patterns in autumn and verified by quantitative molecular data. Indigenous people can contribute data on the coat patterns of caribou in different populations.

Data interpretation

An important step is the interpretation of data. The scientist and the indigenous person may come to the same conclusion but by different processes. For example, fatness in caribou may be caused by an early spring and low number of flies. The indigenous hunter may know from many years of experience what environmental conditions result in fat caribou. It may take scientists many years of painstaking work and large budgets to arrive at the same conclusion. Scientists use statistics and computers to sort out which environmental variables are most important. Experience is also valuable in coming to correct conclusions. The results of other researchers must be drawn upon to fill gaps in information. However, care must be exercised in transferring data among populations and regions.

Data transfer

Information on wildlife was spread orally in indigenous societies. It was important for survival. Technical data are transferred in reports and publications. Information is also transferred orally in talks, lectures, and interviews. The accumulated information on a subject is termed baseline data and all new data are discussed in terms of previous work.

Management action

Wildlife management must involve a mix of technical and indigenous knowledge where indigenous people are the primary resource users. This is the step where co-management is most effective. The technical information is presented and the indigenous users see how it fits with their observations. If there is consensus on the validity of the data, then solutions to problems are solved jointly through discussion. The indigenous members know what types of management actions may be successful in their communities and hunting areas. Imposition of solutions by technical managers will not work unless the local people support them.

The evolution of co-management

Why did co-management solutions not arise until recently? The biologists, with a few exceptions, did not believe that the natives could help them gain knowledge. In turn, the natives often believed that they knew more about caribou than any biologist. Both were correct: the biologists knew certain facts unknown to the natives and vice versa. There were and are language barriers. The scientific managers did not think that hunters were interested in the complicated technical methodology used to arrive at management decisions. Co-management could not work until both parties had an understanding of the value of each others' contribution. Their methods of obtaining information (Table 1) and solutions to management problems are similar.

The minimum requirement for co-management is: (1) direct involvement of indigenous people in management decisions and means of acting on them; and (2) direct involvement of native people in data gathering. Wildlife management boards are a means of achieving the first requirement. Native people were involved in many wildlife studies, but mostly as assistants. They should be more involved in project planning and interpretation of results. Furthermore, scientists and resource managers should devise systems of collecting data and ecological information from indigenous people. There may be no proof of ecological relationships suggested by the local people but repeated observations from different groups would suggest relationships and these could be tested scientifically. Some types of monitoring such as fatness and general health of caribou populations and sub-populations can largely be done by the hunters.

It is true that the native people have had to adapt to the scientific form of data gathering and the solving of management problems in semi-formal meetings. There was no apparent alternative considering the large number of native communities involved and no system of collecting adequate traditional information.

Table 1. Major similarities and differences between the indigenous tradition and the scientific method of data gathering and processing and major conservation/management methods.

Process	Indigenous tradition	Scientific method
Data collection	Qualitative, empirical observations	Formalized, empirical, quantitative observations
Data accumulation	Brain, oral tradition (stories, legends)	Forms, tables, computer data bases, reports, publications
Data analysis	Discussion	Statistics, computers, brain predictive models
Data interpretation	Inductive reasoning	Results vs. those of others; induction and deduction
Data transfer	Oral	Reports, publications, oral
Conservation/ management method	Consensus to reduce kill through social pressure, taboos	Regulations to reduce kill, predator control, habitat protection, education

Adaptive management

McDonald (1988) suggests use of adaptive management techniques to aid wildlife management in the North. The essence of the method is trial and error management. Such methodology appears to have little application to caribou management because: (1) the system is more stable than suggested even though it is a rather simple system: essentially one prey and two predators including humans; (2) there is little scope for experimentation (e.g., wolf control or altered harvest); (3) measuring the effects of any "tinkering" is exceedingly difficult and expensive (e.g., effect of wolf control in the 1950s and early 1960s); (4) the key indicators (hunting and wolf mortality) are known; (5) experimentation with habitat can have long-lasting effects (e.g., experiments of minimum winter habitat requirements could have 50-70-year effects). These techniques are more applicable to closed systems such as lakes where the effects of manipulating ecological and human factors can be readily measured. The co-management aspects in adaptive management techniques are good.

The first caribou management board

The first major study of caribou between Hudson Bay and the Mackenzie River in 1949–51 indicated there were 677,000 caribou, far fewer than at the turn of the century (Banfield 1954). Numbers dwindled during the 1950s and led to the first caribou "crisis". Predator controls were initiated. By 1957, numbers in what is now known as the Beverly herd were estimated at 100,000 (Kelsall 1968). We know from comparisons between visual and photographic surveys (Heard 1985) that numbers were probably 2–3 times larger than the estimates. They had to be to support the annual kill. The first crisis led, in 1957, to formation of the Technical Committee on Caribou Preservation (TCCP). Members were from the Department of Indian Affairs and Northern Development (DIAND), the Canadian Wildlife Service (CWS), and wildlife agencies in Saskatchewan and Manitoba. The members from CWS and Saskatchewan joined forces in May 1967 to mount a 17-month study of the Saskatchewan herd (part of the Beverly herd) (Kelsall 1968). Research on fire (Scotter 1964) and discussions at the TCCP led, in 1967, to a 5-year program of firesuppression on the winter range of the Beverly herd in the NWT. Field stations were established at Porter and Sandy lakes. In spite of having crews on the range, large areas of the herd's winter range burned in the NWT in 1970 and 1971.

Beginning in 1958, the caribou herds began to recover and by 1967 the estimate was about 160,000 for the Beverly herd (Thomas 1969). Still, numbers were relatively low in the Kaminuriak herd leading in 1966–88 to a major study of that herd by CWS. The herd was believed to be stable at 63,000 (Parker 1972). By 1973, the TCCP could not justify its further existence and it disbanded. There was, at the same time, an Administrative Committee for Caribou Conservation that was inactive.

The second caribou board

Increasing concerns for caribou management in the 1970s led to formation of the Caribou Management Group (CMG) in 1978. Membership of the CMG was the management agencies of NWT, Saskatchewan, and Manitoba, plus DIAND, the native affairs agency and land manager in the NWT. Observer status was conferred to CWS in 1979 and membership in 1980. Several events combined to spark formation of the CMG and its successor, the Beverly and Kaminuriak Caribou Management Board (BKCMB). Survey data indicated that the Kaminuriak herd was declining. Native people in Baker Lake blamed mining explorations for changes in caribou distributions and some decline in numbers. In 1977, they launched a court case against the mining companies and the Government of Canada to stop the mining explorations. In 1978, controls were placed on mining explorations within caribou protection areas on the calving grounds of the two herds. In 1979–80, concern was extended to the Beverly herd because of the large kill in Saskatchewan. In 1979, the CMG decided that herd management was not possible unless the user groups were involved and supportive of management plans. In this paper "user" refers to mostly native people that use the caribou resource within the historical ranges of the Beverly and Kaminuriak herds. Native leaders, Gunther Abrahamson (DIAND), and Rich Goulden (Manitoba) spearheaded formation of a board with native and government representation.

Interviews with native users in 1981 and 1982 editions of *Caribou News* indicated that causes of caribou declines and possible solutions were similar to those proposed by government managers. The users tended to place more emphasis on the effects of fire and industrial activities; the biologists on the effects of hunting. It was clear, however, that management by quotas or other restrictions would be impossible unless the users were involved in the decision-making process. Voluntary reductions in the kill would not occur as long as responsibility for caribou rested with governments. Nor was token representation by users acceptable. Trade-offs often were mentioned: if users were to be restricted then they must receive some concessions in return. These concessions might include increased fire protection, predator management plans, or intersettlement trade of caribou and other "country" foods.

The Beverly and Kaminuriak Caribou Management Board

Inception, composition, and function

The main landmarks in formation of the BKCMB were: (1) a ministerial meeting in Winnipeg in December 1980 where a crisis situation was acknowledged; (2) user meetings in Snowdrift, NWT (April 1981); and user-government meetings in Thompson, Manitoba (June 1981), and Prince Albert, Saskatchewan (August 1981); and (3) negotiations between users and governments in Yellowknife in October 1981. In response to a ministerial letter to native groups that cooperative action was needed, the users decided in the Snowdrift and Thompson meetings they would form their own caribou management board. The DIAND Minister agreed to fund only a joint user-government board. The final agreement saw government participation in a board dominated in numbers by users.

The Board became official on June 3, 1982, with ministerial signing of a 10-year agreement. The agreement was among four governments with Canada represented by the ministers of DIAND and Environment. Users agreed to a joint board provided they could have two representatives from each of the geographical areas of South Slave and southern Keewatin (NWT), Manitoba, and Saskatchewan. User representatives are appointed by the respective jurisdiction ministers and most of their Board-related expenses are paid by those agencies. Meeting locations rotated and included a user community about every second meeting. Each agency contributes $15,000 per year to fund Board activities. Beginning in 1989, the board decided to hold two of the three meetings per year in the user settlements.

The Board functions largely through consensus or near-consensus achieved through modification of a position through considerable discussion. A motion is raised and voted on by raise of hands. A few key issues such as commercial quotas were determined by secret ballot. The Chairman votes only in the case of ties. A Secretary/Treasurer was hired by the Board and that person is essentially an Executive Secretary who handles many of the administrative functions. Written operating procedures of the Board are updated periodically. The process, including the need for audited financial statements, seems unnecessarily structured to user representatives. However, much of the "bureaucracy" is a condition of government grants to operate the board.

Objectives, duties, and responsibilities of the Board

Board objectives (condensed) as specified in the Beverly-Kaminuriak Barren-Ground Caribou Management Agreement are to: (1) coordinate management of the herds in the interests of traditional users; (2) establish a process of shared responsibility for the development of managements program; (3) establish communications to further conservation and habitat protection; and (4) discharge management responsibilities collectively (Beverly and Kaminuriak Caribou Management Board 1987). The objectives clearly indicate that coordinated, cooperative management (co-management) of the herds is primarily for the benefit of the users. This was an ideological change from earlier emphasis on conservation. This point is important because it places the emphasis on managing at a high sustained yield rather than imply preventing the herd from dropping below a certain population size. A summary of the Board' s duties and responsibilities are to: (1) recommend measures that will restore the herds to a size that will meet the requirements of traditional users; (2) maintain habitat; (3) communicate Board functions to user groups;(4) discuss management plans with governments and users; (5) submit annual reports on the state of the herds and Board activities; and address other matters affecting the herds. The duty of the Board clearly is to maintain the herds at population levels that will meet the requirements of the traditional users. The actions of the Board are guided by terms of the agreement and a management plan.

The Beverly and Kaminuriak Caribou Management Plan

Background

The need for a plan to guide the Board was realized as early as 1979 and various groups drafted preliminary editions of the plan. After formation of the Board, subcommittees that included user representatives worked on the plan and it passed through many revisions. The Board hired an academic to bring the plan to a conclusion in 1986 and printing in 1987 (Beverly and Kaminuriak Caribou Management Board 1987). The plan was developed slowly because the Board wanted all parties to be satisfied with its contents. The plan received approval at a user assembly held in Eskimo Point and it was widely distributed throughout Canada.

Goals, objectives, and principles

The mandate, goals, objectives, principles, and actions of the Board are outlined in the plan. The goals are to safeguard the herds: (1) for the traditional users and (2) for Canadians and others. There are important objectives: (1) to maintain each herd above a crisis level of 150,000; (2) to achieve optimum herd sizes of 330,000 (BH) and 300,000; (3) to ensure herd accessibility to users; (4) to increase knowledge of caribou ecology; (5) to encourage wise use; (6) to involve local people in management; and (7) to strengthen public support for caribou conservation.

Ten Board principles relate to cooperation, communication, co-management, herd conservation, the food and cultural value of caribou, efficient use of caribou, local participation, maintenance of habitat, the central role of the Board, and to ensure that caribou are considered in all land-use plans.

Action plans

The manner in which the Board will attempt to achieve its goals, objectives, duties, and responsibilities are set out in 15 action plans. They are outlined under the headings: (1) information, education, and communication; (2) supply of caribou; (3) use of caribou; and (4) protection and habitat management. Each plan is discussed under the headings: background; problem statements; objectives; methods; schedule; budget; evaluation; and lead role. Most of the action plans are ongoing such as *Caribou News*, Board liasion, competitions and awards, herd size and recruitment, spoilage of meat, crippling losses, fire management, protection measures, and caribou-human relationships. The schools program was completed but work is underway on improving its implementation. The study of herd definition (Kaminuriak) was completed but more work is needed. The requirement for caribou must be revised periodically; priorities for demand were established in 1987. The study of the effects of fire is nearing an end but additional monitoring is needed.

The Board reviewed the progress of the action plans in August, 1988. However, responsibility for the plans rests with the Board or the jurisdiction heading the plan and accountability is not rigorous. The plan for the Porcupine herd includes specific management objectives (e.g., obtain recruitment data in March/April) throughout the year (Porcupine Caribou Management Plan n.d.). Cized (n.d.) and Scotter (in press) provide additional details on Board functions and processes.

Board accomplishments

Communication within the Board

The Board is a forum for the views of user and government representatives and various observers who attend meetings. Data obtained on the herds is presented at meetings and discussed. Observation of user members are brought forward to complement the reports of biologists. These range from information on movements and the fatness of different groups of caribou to behaviour of caribou in response to various activities on the land. This exchange is probably the most important function of the Board, at least in the short term.

Communication among governments, users, industry, and others

The Board serves as an important communication link among the four governments and their agencies as well as between them and the various user groups. Perhaps more valuable are the exchanges among the native groups. They realize that harvests in one area can affect the take in another region. Fires in northern Manitoba may affect the distribution of caribou in the Keewatin. One group may have abundant caribou; another group little or none. Native representatives exchange information on factors that affect the caribou throughout the range rather than in their own particular area. In user communities, an evening session of the Board is devoted to communication between the Board and the users. The meetings are vital to conveying the purposes of the Board and the major concerns of the community elders. The Board was used by industry to attempt to bring changes to regulations affecting mineral exploration on the calving grounds of the herds. Hunting associations make requests to the Board concerning caribou quotas for non-native residents. Thus, the BKCMB is a clearinghouse for communications concerning the two herds.

Caribou News

Caribou News was first issued in May 1981 before the Board was established and largely through the influence of officials in DIAND who financed a large proportion of the costs. Current costs for six issues are $100,000 per year. The management agencies contribute to costs in proportion to the number of issues sent to communities in each jurisdiction. The original intention was to publish the bimonthly *Caribou News* for 2 years to inform users about the purposes of the board, to inform the interested public, and to attempt to change attitudes. The paper proved to have popular appeal as well as great value and continued to publish for 10 years. Prevailing financial restraints may see *Caribou News* come to an end in 1992. The paper maintains an independent stance from the Board. The paper includes information on Board activities, research efforts, settlement activities, and stories of general interest of caribou managers and users.

Schools program

A major initiative and expenditure, that began in 1984, was development of a Schools Program consisting of four modules. Each unit contains written materials, tapes, and slides. It was intended for use in each school within the range of the two herds. An independent evaluation of the schools program indicated that it was successful (Nortext 1987). It was found by field representatives to receive enthusiastic use by some teachers in some schools. A survey of use in 1989-90 in northern Saskatchewan indicated that 13-20% of teachers used the kits for 4-5% of instructional time (Nicholls pers. comm.). An educator invited to a Board meeting suggested ways to improve use of the material. The prime problem was that use was discretional; the program was not integrated in the curriculum. Steps are now being taken by the Board to remedy the problem. There appears to be need for new content and material aimed at lower grades.

School competitions/awards and schoolarships

The Board realized that the future lay with youngsters in school. A schools competition was started in 1988 with the objective of making the Board known to youngsters and to get children thinking about caribou, their uses, and management. Prizes are awarded after judging is done by Board members. Many members were amazed by the quality of the art, poetry, and prose. Some of it was published in *Caribou News*, which then makes the paper interesting to the students.

The Board also supports studies of caribou and related subjects through a scholarship fund established by the Board and augmented by a grant from the NWT government. The fund legally is separate from the Board but its trustees sit on the Board. About $3,000 are awarded annually to one to three recipients.

Video and radio programs

The Caribou Management Group commissioned production of videos in 1980 that explored all sides of the caribou management problem. This approach was new in the north and its success was due to involvement of Inuit and Inuit groups in its production. The videos were shown to Inuit communities in 1981 and 1982. The high costs prevented its extension to communities in northern Manitoba and Saskatchewan. In 1989, the Board supported production of tapes that were broadcast on northern radio stations. The tapes were information items by biologists and managers.

Cooperative research

The Board has facilitated cooperative studies of the two herds. For example, a user Board member has piloted an aircraft containing surveyors from the governments of Manitoba and the NWT. The timing of caribou surveys by biologists of Manitoba, Saskatchewan, and CWS was coordinated so that coverage was complete from Yellowknife to northern Manitoba. The Board supported financially a values-at-risk study that incorporated fire maps into a computer-based geographical information system (GIS). The management agencies will be able to update the GIS annually. Analysis of burn trends and how they will affect caribou and other wildlife will be facilitated by GIS capabilities. The GIS will aid decision making if fires are fought on the caribou range. Cooperative research is not an action plan but it is implied in Board objectives.

Priorities for use of caribou

In April 1987, the Board formally etablished priorities for use of the two herds. The order is as follows: (1) traditional users, domestic use; (2) resident users, domestic use; (3) traditional users, intersettlement trade; (4) traditional/resident use for non-resident hunting; (5) commercial, local; and (6) commercial, export. These priorities are important because they focus on the importance of caribou for subsistence by traditional users (mostly natives) and they formalize a reverse order of removal when caribou numbers decline. Priorities may have to be reordered in the future. For example, sports hunting could generate millions of dollars into local economies with no adverse effect on the caribou population. Native corporations must be major stakeholders in such developments.

Caribou protection: stands on developments

The BKCMB has lobbied DIAND to retain the Caribou Protection Measures that began in 1978 and provide for minimum disturbance of caribou in the two herds during spring migration (May 15–June 15), on the calving grounds (June 1–30), in post-calving areas (June 15–July 15), and at major water crossings. Funding from DIAND for monitoring the regulations currently is $65,000 per year.

The Board keeps an eye on and reviews new developments that could affect the caribou. For example, in 1985, members reviewed the proposal for a powerline from Beaverlodge (Lake Athabasca) to Wollaston Lake. The Board reviewed the plans for fighter aircraft training runs at low level from the region of Artillery Lake to Fort Chipewyan. The Board has taken strong stands against opening the Thelon Game Sanctuary to mining and to development of an uranium mine (Kiggavik) west of Baker Lake.

Fire management

The Board, in 1984, requested that government agencies fight fires on the winter range of the two herds. The agencies responded that they had insufficient funds to extend fire control. Several millions of dollars would be needed to establish the infrastructure for effective fire suppression on the winter range of the Beverly herd in the NWT. Results of a fire study indicated that fire suppression was not needed at the caribou population level (Thomas 1991). However, the distribution of the Beverly herd was affected by burns in the past 50 years or longer. A management objective is to ensure access to the herds by traditional users. This cannot be accomplished unless a high proportion of the forests around villages is maintained in ages older than about 70 years. Priority areas for the users are their traditional hunting and trapping areas. Users in all southern communities, such as Fond du Lac, Black Lake, Wollaston Lake, Brochet, Lac Brochet, and Tadoule Lake have to go further and further north to obtain caribou.

Accomplishments relative to goals and objectives

In general terms, all Board objectives, duties, and responsibilities (p. 6 & 7) were attained. Management plan goals were satisfied. Some of the management plan objectives were met: maintaining the herds above 150,000 (objective 1); to encourage wise use (objective 5); and to involve local people in management (objective 6). Objective 2 of achieving herd sizes of 330,000 and 300,000 may have been reached in the mid 1980s. The latest estimates of 190,000 ± 71,000 (standard error) (Heard *et al.* 1990) and 220,000 ± 72,000 (Heard and Jackson 1990) for the Beverly and Kaminuriak herds fall below that value. The confidence limits of the estimates (ca. double the standard errors) overlap the population goals. No actions were taken on ensuring herd accessibility to users (objective 3). Accessibility generally was good for Inuit communities and for Snowdrift. Herd accessibility to communities in northern Manitoba and Saskatchewan has eroded with forest fires being the apparent primary cause. The objective of increasing knowledge of caribou ecology (relationship to the environment) was met to some degree by the results of the fire study. Ecology of caribou in the spring, summer, and autumn is poorly understood. The degree to which public support for caribou conservation was strengthened remains unknown.

Reasons for board successes

The management plan

The management plan even in draft stages served as a guide for Board actions. The plan gives timetables for various actions. It provides a constant reminder of the goals, objectives, and responsibilities of the Board as spelled out in the agreement and the management plan.

Chairmen and vice-chairmen

The Chairman has a great responsibility to attempt to achieve consensus on issues. He must understand viewpoints of users, scientists, managers, governments, and the general public. Traditionally, users avoid snap decisions and generally prefer decision by consensus. Their decision making is based on serious thought of all the consequences of a certain action. They prefer prolonged discussion that includes elders in each community. The Chairman must be patient and draw comments from user representatives. Decisions often are postponed to provide sufficient time for discussion and consensus. Much of the success of the Board is because Chairmen and Vice-Chairmen were able to weld the diverse representatives into a common purpose through prolonged discussion.

Native representation

Success of the BKCMB is largely due to the user's choice of their representatives. On certain issues, such as commercial use of caribou, they tolerate majority decisions that go against their personal convictions and those of communities they represent. They have shown great patience in how long it takes to obtain action on certain issues. For example, since 1982 native representatives from treed regions of the range have requested that the management agencies fight forest fires. Little action was taken. The representatives generally are deeply concerned about the caribou and their proper management.

Membership continuity

Turnover of members was low: the first Chairman served for 8 years; two user members for 9 years; and each government or department was represented by 2-4 members. Continuity is important and alternate members should receive a good briefing before attending meetings. Detailed minutes record board discussions and decisions. A brief summary of major decisions and discussions relative to each action plan and to "other business", updated after each meeting, would be useful to continuing members and particularly to alternate and new members.

Spirit of cooperation

Cooperation has been good because agency representatives and users realize that they have the same objectives. The agencies have other clients when herd numbers are high. For example, in 1988, the Board approved a request that the quota for residents of the NWT be increased from two to five caribou. Two user groups sought from the Board and received approval to sell caribou within the NWT. Commercial use was allowed in the NWT for many years but only among holders of General Hunting Licences. The selling of caribou to others in the NWT was restricted to trial quotas of 200 and 350 caribou for Hunters and Trappers Associations in Fort Smith and the Keewatin, respectively. Later, the Board approved export of up to 100 caribou in the Keewatin quota for Inuit consumption in southern hospitals. The requests for commercial quotas were approved only after the population trends indicated that the herds could withstand limited commercial use. The quota was not used in Fort Smith. Generally, user members from Saskatchewan and Manitoba are opposed to any commercial use of caribou and hunting by "residents" and "non-residents". Thus, there is no non-resident hunting of the two herds, whereas non-resident hunting on the adjacent Bathurst herd generates $1.4 million. The replacement value of meat obtained from the Beverly and Kaminuriak herds is $13-14 million. Cultural, recreational, biological, and intrisic values are incalculable.

The herd's productivity and distribution

The BKCMB has not had to address caribou shortages except locally. Recruitment in the Beverly and Kaminuriak herds in the late-1970s and 1980-s has averaged 17.4 (Bh) and 17.6% (BKCMB 1987, Williams *et al.* 1990) compared with 16% in the 1950s and 60s (Kelsall 1968). Large numbers of caribou have not migrated far into Saskatchewan or Manitoba since the early 1960s with the exception of 1 or 2 years (e.g. 1979-80 in Saskatchewan, 1987/88 in Manitoba). Therefore, the estimated average annual retrieved kill from the two herds (20,000) was much reduced from what it might have been. The actual mortality to hunting is 25,000 caribou if 20% is added to account for crippling and unretrieved animals.

Problem areas

Technical problems

Technical problems identified by Therrien (1988) for the Porcupine Caribou Management Board also apply to the BKCMB: little control of techniques used; no control of budgets; no control of implementation; no guarantee of user involvement; and no independent research capability. The precursor CMG (1978-82) was supported by a technical committee comprised of biologists from each agency. There was no provision for such a committee upon formation of the BKCMB. The Board has requested advice from ad hoc meetings of agency biologists on two or three occasions. Technical aspects generally are handled by each jurisdiction. Problems arise from this arrangement. The Board is not certain if the data obtained for the herd are adequate for management purposes. For example, management may be impossible if population (excluding calves) estimates are obtained every 5-6 years, as proposed, with population estimates subject to large confidence limits, e.g., 190,000 ± 142,000 for the Beverly herd in 1988. The change from visual surveys to photographic-based surveys improved herd estimates but the large confidence intervals remain. The solution may lie in use of post-calving photographic estimates as used on the Bluenose and Porcupine herds.

Population trends could be followed if better data were available on retrieved kill, the extent of wounding, the natural mortality rate, changes in age structure, and recruitment. Not much has changed since Fuller (1979) stated that the quality of the data was wholly inadequate for the management of caribou. The factors that influence caribou health, physical condition, and natural mortality are poorly understood because a comprehensive, long-term study that evaluated the importance of alle ecological factors has never been done. Every 2-3 years, the BKCMB should seek independent advice from recognized authorities from outside the Board on the adequacy of data being obtained in support of Board objectives. The best format would be a structured yet informal workshop where users would be represented and contribute. The scientists, with the assistance of users, have the capability to produce data that could be used to effectively manage the caribou herds primarily for the benefit of traditional users. Lack of adequate funding and perceived restrictions on techniques prevent them from doing so.

Membership

A complaint of user groups is that the representatives from government have no power. The government representatives usually are either biologists or first or second-level managers. While they may be knowledgeable of caribou, they are unable to commit their agencies to new actions. Conversely, user representatives typically are Chiefs or heads of user associations. They are part of, or close to, the decision making level in their communities or region. The problem is that few senior managers in government are familiar with caribou ecology and management. This is solved to some extent by having agency biologists present to support the manager. User members sometimes believe that the government members are not free to use their best judgement on certain issues and must adhere to policy established by their department or governments.

Attendance generally is good at most meetings despite two problems. Self-employed members lose revenue during the 4-6 days needed to attend meetings. Travel costs can run as high as $2,500 per meeting for some members. Cost could be reduced by meeting Thursday-Saturday and scheduling informal tours and events on Sunday.

Communication

The greatest communication gap between the board and the user community appears to be between user representatives and the communities they serve. The function of the Board is not understood in the communities as revealed at public meetings. How this problem can be resolved is not readily apparent. One possibility is weekly local or regional radio shows devoted to wildlife and including the last information on location of wildlife, hunter success, as well as wildlife research and management. The show would have to be locally produced in local languages. User representatives may need the advice or assistance of educators in finding ways of getting the message out. Further, *Caribou News* is unlikely to exist after June 1992. It is the main communication vehicle between the Board and the users. The Board would like to have every resident in user communities familiar with its purpose and function. That may be an unrealistic goal. Few southern residents are familiar with the wildlife management programs that affect them.

The Board has not addressed mechanisms to systematically obtain the user's knowledge. This knowledge should include the collective wisdom of elders and current information about the distribution, movements, health, fatness, and reproduction of caribou. Additional information could be accumulated on the behavioral responses of caribou to burns, snowmobiles, aircraft, and other forms of disturbance. One possibility is to process the data using "expert systems" computer technology.

Accountability

There is little accountability for seeing that action plans are completed on schedule. The Executive Secretary sees that outstanding issues are placed on meeting agenda. There is provision in the Plan for an annual review at the March/April meeting.

Looking into the future

Expiry of the Agreement, June 1992

Budgetary cycles mean that a decision on whether the agreement will be renewed in June 1992 will be made by autumn 1991 or earlier. In December 1990, the Board contracted a consultant to review the success of the BKCMB in meeting its goals and objectives. Reporting dates are March (interim report) and August, 1991. The review will not be an audit or value-for-dollars exercise. Most Board members appear to favour an extension of the Board's mandate.

Land settlements and other wildlife management boards

Some members see the Board's function being replaced by wildlife management boards arising from land claims settlements. Others see a continuing or greater need for an inter-jurisdictional board on caribou management, as the caribou ranges are further subdivided along political lines. The Board could encompass all inter-jurisdictional wildlife management with caribou being the most important trans-boundary species. The logical solution is for some representatives to be on two or more boards concerned with wildlife management and land use. Some members of the BKCMB currently sit on other boards. There is increasing communication among boards through visitations: invited, requested, and casual. Ideally, the political units should correspond with herd boundaries as they did before Europeans arrived (Gordon 1975).

Politics: Imbalance of government and "User" representatives

If they so desired, the users through their majority could dictate all deliberations of the Board. This has not occurred to date because issues have not divided along user-government lines. Users realize that the Board is only advisory and members have accepted the futility of confrontations. The goal of both groups is the same - to maintain and possibly enhance a major, natural, sustainable, renewable resource. Members must strive to keep the Board as apolitical as possible. The Porcupine Caribou Management Board has balanced government and user representation, however the user population is much smaller than that encompassed by the BKCMB.

The next caribou crisis

The first board, the TCCP was disbanded in 1973 because the herds increased during the 1960s. Within a few years, caribou apparently declined once again and the Caribou Management Group was formed. A repeat of history could happen if the Board disbands in 1992. Caribou numbers fluctuate in response to weather and weather-related factors as well as to the level of the kill and predation. The question is not if the herds will decline again but when. The present kill appears to be the maximum that the herds can support. Calf production has been high in the 1980s and wolf numbers relatively low. Wolf numbers were relatively low on the winter ranges of the two herds in the 1980s. Any downturn in recruitment caused by weather factors, directly or indirectly, or an increase in wolf numbers could result in caribou declines. The test of the Board will be its ability to manage the herds when the next crisis arrives.

Better herd data

The best-possible monitoring of the herds and their utilization will be necessary if they are to be maintained at a high and valuable level. As mentioned earlier, more-precise data are needed on population size, recruitment (including standard errors), and kill (e.g., no data for Snowdrift). Data are needed on movement patterns, winter distributions, natural mortality factors and rates, behaviour to disturbances, spring and summer ecology, and genetic differences among populations, among others. The Chipewyan elders believe that caribou should be left alone. These beliefs currently inhibit data collection in support of technical forms of wildlife management. For example, radio collars on caribou would help to define herd boundaries; to measure herd interchange and gene flow; to support survey techniques based on post-calving photography; to measure natural mortality rates; to record behaviour towards burns, roads, aircraft, skidoos, minig developments; etc.

Intensity of herd management

There is little active management of the herds. There are no restrictions on most native users except Metis users in the provinces. The quota for "residents" of the NWT (minimum 2 years residence) is adjusted from time to time from two to five caribou. The take of caribou from the Beverly and Kaminuriak herds by non-native residents is minor or insignificant. Caribou hunted along the winter road to Contwoyto Lake may belong to the Beverly or Bathurst herds. There is no "sports" hunting except by residents in Manitoba (150 tags). The information campaigns sponsored by the BKCMB, including preventing wastage of meat, "pick your target", etc. has unknown influence on users out on the hunt. Other factors such as herd distribution and movements, the cost of air charters, the availability of winter roads, snow conditions and other weather factors, the price of furs, and the number of wolves, has more to do with the size of the harvest than the management actions.

A time will come when increased kill and/or high natural mortality will cause herd reductions. The user communities are presently doubling in numbers in 18–24 years (3–4% annually) (Hamelin 1979, Fuller and Hubert 1981, Special Committee on the Northern Economy 1989). Minimum user needs are in the order of 3 caribou per person or 20 caribou per family.

Retrieved kill per successful hunter, per hunter, and per person in the Kitikmeot (Central Arctic) Region in 1982–84 were 42, 15, and 3.1, respectively (Jingfors 1986). The estimated total harvest was 3.6 caribou per person in the first year of the study. Jingors (1986) calculated that per capita harvest was 3.2 and 2.8 caribou per year in a similar harvest study in Keewatin Region in 1981–83 (Gamble 1984). Wants are listed as high as 5–7 caribou per person (Miller 1982) and 30–40 caribou per family. There may soon be a need to manage the herds more intensively as suggested by Fuller and Hebert (1981). There are two major options that will challenge the Board: (1) reduce or change the age/sex structure of the kill; and /or (2) reduce predation. Minor options include safeguarding habitat and reducing disturbances. These are important but currently have little effect on herd numbers. *The main challenge is to not allow the herds to sink below present levels because recovery takes many years and it will be painful to the users.*

User requirements must be projected and caribou population sizes managed to support the required level of use to limits imposed by the environment (forage/snow).

Habitat loss/modification

The greatest long-term threat to the two herds is loss or modification of habitat. Loss of habitat is most likely to be caused by greater burn rates because of changes in weather. The global warming trend could have such an effect. Modification of habitat is caused by a variety of developments including roads, pipe and power lines, mines, and tourism as it may affect harassment particularly at water crossings. Of these, the most potentially damaging are roads that increase access to the herds and increase the kill. Hunting along roads could affect movement patterns over time. Potentially as serious as roads are global air pollutants that could damage lichens or make caribou meat unfit for consumption. Prevailing winds mean that contaminants from the U.S. and southern Canada are a problem only for short periods each summer. Global pollutants are a concern. Radio-cesium from the Chernobyl accident in the U.S.S.R. was deposited throughout Canada. Lichens in Finland are affected significantly by pollutants from other countries.

Conclusions

1. Effective management of the large migratory populations of caribou was not possible until mechanisms of co-management were established.
2. Wildlife management decisions and mechanisms should occur with technical and user groups sitting around the same table.
3. If caribou management occurred before Europeans arrived in Canada, the ways were lost because of lack of a written history and changes wrought by the immigrants. Conservation measures such as use of all the carcass were tied more to survival than to modern concepts of management.
4. No benefit is gained from attacking the indigenous and scientific forms of data gathering and management; clearly the best elements of both should be united in a system of management that will work in the North.
5. There are similarities in indigenous and scientific systems of data collection and interpretation and in decisions about how conservation/management may be effected.
6. Major differences in the two systems relate to reliance on qualitative and quantitative data by indigenous people and scientists, respectively; to traditional scientific methodologies of data accumulation, analysis, interpretation and transfer; and to greater use by scientists of deductive as opposed to inductive reasoning.
7. An advisory caribou management board comprised of eight Dene, Metis, and Inuit members and five representatives from three governments has, since 1982, achieved many of it's goals, objectives, and responsibilities.
8. Board successes are attributed to development of a management plan; to the quality of founding members; to relatively low turnover of members; to understanding Chairmen/Vice-Chairmen; to a spirit of cooperation; and, perhaps most importantly, to excellent cooperation by the caribou herds.
9. Board shortcomings include lack of control on technical matters; lack of a strong technical committee to guide the Board; inadequate communication within many of the communities; failure to establish a process whereby information on the herds is consistently obtained from the many users;

and limited power to ensure that action plans are completed.

10. The future of the Board depends on its: renewal of the agreement in 1992; links with other wildlife management boards; ability to remain apolitical yet pro-active; ability to stave off harmful developments; ability to manage at low population size; ability to better monitor the herd' s status; and ability to manage more intensively to meet, as far as possible, the needs to traditional users.

Acknowledgements

We received many presented here from discussions with other members of the BKCMB and fellow workers. We thank A. Gunn, G. Abrahamson, P. Usher, and R. Edwards for manuscript reviews.

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Co-management in action: The Porcupine Caribou Management Board

Doug Urquhart & Albert Peter.

Porcupine Caribou Management Board, Site 20, Comp. 116, R.R. No. 1, Whitehorse, Yukon Territory, Canada Y1A 4Z6

Abstract: The Porcupine Caribou Management Board is typical of co-management boards in northern Canada. It is composed of 8 members representing governments and user groups plus a chairman and secretariat who are officers of the Board. The main function of this Board is to permit significant input from user communities to the management of the Porcupine Caribou Herd. To do so, the Board develops recommendations for management of the herd wich are provided primarily to the territorial Ministers of Renewable Resources.

The success of the Board's operation over the past 5 years is due to many factors including astute chairmen, enlightened bureaucrats, dedicated user representatives and a dilligent secretariat. Together this group has excelled in communication with the user communities, development of a relevant management plan plus a variety of other projects aimed at increasing user involvement with the system. So far, all this has been accomplished with friendliness and respect among members and their constituents and the full support of government funding parties. Much of this is due to the Board's style of operation which sincerely attempts to blend native and bureaucratic approaches to decision making.

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