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Ecological role of hunting in population dynamics and its implications for co-management of the Porcupine caribou herd

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Abstract: At a present population size of 160 000 animals, the Porcupine caribou herd has been subjected to an annual harvest rate of 2% for the past couple of decades. We modeled potential sensitivity of herd population dynamics to hunting and used that relation as a basis for a herd monitoring system. Maximum number of adult cows that could be harvested without causing a subsequent decline in herd size was calculated as a function of total number of adult cows in the herd and recruitment of calves to yearling age-class. Maximum cow harvest, therefore, is a threshold above which hunting has destabilizing effects on herd dynamics. Actual harvest in relation to theoretical maximum harvest provides a basis for prediction of herd sensitivity to hunting. Maximum harvest is a linear function of recruitment. Herd dynamics are especially sensitive to low recruitment, however, when combined with low herd size. The two relations involving recruitment and herd size provide the basis for predicting herd dynamics and sensitivity to hunting. Herd size is best estimated by aerial census, while an index of recruitment can be predicted by monitoring autumn body condition of adult females. Body condition can be estimated on the basis of a few simple metrics measured by hunters in the field. The hunters' data on body composition, combined with aerial census data on herd size, provide a useful tool for managers and co-management boards to devise policies and regulations to manage the herd. The population model and monitoring system can operate on the Internet and be accessible to all users in villages within the range of the Porcupine caribou herd.

Key words: Alaska, caribou, monitoring system, Northwest Territories, population model, *Rangifer tarandus,* Yukon.

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Introduction

"Co-management" systems for managing human exploitation of common-property natural resources are becoming increasingly popular in rural and remote regions of the world (Berkes *et al.,* 1991, Pinkerton, 1994). They are based on the assumption that user-groups involved in management decisions are more likely to comply with harvest limitations than if limitations are simply dictated by a governmental authority. Voluntary compliance with regulations is especially important in remote regions where legal enforcement is logistically or administratively difficult. Co-management systems, therefore, hold prospect for much of the world's underdeveloped regions. They also offer potential for reducing political conflicts over natural resource management in developed regions where perceptions of needs differ between local residents and geographically distant administrators.

Klein & Kruse (1996; Klein *et al.,* 1999) recently studied effectiveness of co-management in application to caribou (*Rangifer tarandus*) harvest systems. They compared user (rural hunters) and manager (government agencies) perceptions of management effectiveness in two contrasting systems: the Beverly and Qamanirjuaq caribou herds in Canada, compared with the Western Arctic caribou herd in Alaska. The Canadian herds were managed by a co-management board comprised of 8 users and 5 government managers, while the Alaskan herd was managed by a state board of game with no direct decision-making by users. Although government managers were found to be more sensitive and responsive to user concerns in the co-management system than in the state-controlled system, the surprising finding was that co-management did not increase the likelihood that users would cooperate with management decisions. The principal conclusion was that co-management boards, alone, cannot substitute for frequent and continued interaction between managers and users at the village level. Users need to understand the rationale for management decisions and be part of the information system that leads to those decisions.

The Porcupine caribou herd is a migratory herd that calves on the arctic coastal plain of northeastern Alaska and winters in the subarctic taiga of northwestern Canada. It is subject to management by both jurisdictions, therefore, but its remote location makes it mostly harvested by local, rural hunters in the Alaskan villages of Kaktovik, Arctic Village, Venetie, and Fort Yukon, and the Canadian villages of Old Crow (Yukon), and Fort McPherson and Aklavik (Northwest Terrirories). The International Porcupine Caribou Board coordinates international issues that affect the herd. A co-management system is employed by Canada's Porcupine Caribou Management Board. There is much interaction between the Gwich'in native villagers on both sides of the international border.

The United States Man and the Biosphere Program took an interest in the Porcupine caribou herd's co-management system in 1996 as an example of co-management harvest systems and their implications for achieving sustainable human society and natural environments in rural areas of the North. Our charge was to investigate the role of hunting in herd dynamics of the caribou and to develop a monitoring system that would provide both historical trend data and prediction of herd sensitivity to hunting.

We expected on the basis of ecological theory that the role of hunting in herd dynamics is not constant or a simple matter of number of animals harvested (Van Ballenberghe & Ballard, 1994; Pascual & Hilborn, 1995). It is critical to the success of any co-management system to understand when effects of hunting may be most important and when they may be relatively unimportant. Furthermore, both users and managers alike should understand dynamic relations. The co-management board needs to know the answers to the following questions: "(1) How big is the herd?; (2) Is it threatened?; (3) Is it healthy?" (Urquhart, 1996). Also, users must be involved in frequent participation with managers in the monitoring and prediction system (Klein & Kruse, 1996). Our goal, therefore, was to develop an analytical system with the following features: (1) is both relatively simple and understandable, (2) requires data input from both users and managers in different but complementary ways, and (3) provides a basis for both monitoring key population factors over time and predicting herd sensitivity to hunting at any given time. Simplicity and practicality come at some expense of technical complexity and precision. We sought to find an appropriate balance that would yield meaningful and useful results.

Materials and methods

Rationale

Recent modeling analyses of the Porcupine caribou herd have revealed adult-female survival and recruitment (calf production and survival) to be the two most sensitive factors affecting the herd's population dynamics (Fancy *et al.*, 1994; Walsh *et al.*, 1995). Recent theoretical analysis of sustainability of harvested populations in fluctuating environments has shown that "threshold harvesting" is most often the optimal strategy for balancing yield against risk of population depletion (Lande *et al.*, 1997). We, therefore, sought an analytical framework that would predict a harvest threshold based on adult-female survival and recruitment rate, where effects of hunting would be considered significant versus insignificant in relation to the herd's size and stability.

We considered harvest threshold to be the maximum number of adult-female caribou that can be harvested (N_{max}) without causing a reduction in number of adult females the subsequent year. N_{max} is a function of total number of adult females in the herd (N_f) and average recruitment of female calves to the yearling age-class (number of spring calves)/(number of non-calves in the population). Thus, N_f times recruitment, minus non-hunting mortality, equals 'harvestable surplus' (N_{max}) of production. Our concept of threshold entails 4 major, simplifying assumptions: (1) Under all harvest scenarios, there will always be sufficient adult males to ensure timely breeding of all estrous females. (2) There is no evidence of density-dependent limitation of the population; thus, survival and recruitment are independent of population density. (3) Location of harvest (e.g., Village A *vs.* Village B) doesn't matter; analysis is based on the entire herd rather than geographic segments. (4) Timing of harvest is not important, except in the case of productive cows killed before autumn while still nursing a calf; hunting of such cows must be treated as a reduction in both adult population and calf recruitment.

We also assumed that only in rare cases are there sufficient data to model a population in its detailed demographics of sex- and age-specific survival and recruitment. A practical, useful model for co-management must be based on data that can be obtained routinely under normal operating budgets and normal amounts of time and effort. We focused on two variables for predicting N_{max}: (1) number of adult females (age ≥2 years) in the population, and (2) percentage body fat of adult females in autumn, which we used as an index of recruitment of calves to the yearling age-class. Number of adult females can be estimated from aerial surveys conducted every three years by government managers. Recruitment of calves to the yearling age-class, rather than recruitment of females to the adult age-class, is a simplification based on an assumed 50:50 sex ratio of calves at birth, equal survival of males and females to age 3 years, and high survival (relative to adults) of 1- and 2-year-olds (Fancy *et al.,* 1994).

Although recruitment is a critical factor, it is very difficult to measure. It is the product of calf production (parturition), early calf survival (to first autumn), and over-winter calf survival. Walsh *et al.* (1995) estimated that sampling efforts would have to be double the efforts of 1994 to detect a 10 percent change in survival for the Porcupine herd. Conception, parturition, and early calf survival, however, are highly correlated with maternal body condition at time of breeding in fall (Thorne *et al.,* 1976; Verme 1977; Cameron *et al.,* 1993; Russell *et al.,* 1998). Females that are in good body condition (high body fat) have high conception rates, low early embryonic loss, and high perinatal survival of their calves (thus high parturition rates). Female caribou exhibit an array of reproductive strategies in association with body condition. Productive females normally wean theit calves in late September. However, if females are not adequately replenishing protein and fat reserves in summer, they can wean calves early, resulting in summer mortality of calves. If female fat reserves are low in early September, calves are weaned and the calves' over-winter survival is reduced. If calf fat reserves in autumn are low, cows extend lactation and the probability of pregnancy is reduced through lactational infertility (Gerhart *et al.,* 1997; Russell *et al.,* 1998).

Indices of adult-female body fat in autumn can be relatively easily measured by hunters (Chan-McLeod *et al.,* 1995). Therefore, we used adult-female body fat in autumn as our predictor, or surrogate variable, for recruitment in calculating N_{max}. Its measurement by hunters complements the measure of total population size by government managers. In our model, linkage between autumn fat and recruitment is through time allocated to lactation. Low autumn fat values are associated with a low percentage of normal weaners and a high percentage of early weaners and extended lactators (Gerhart *et al.,* 1997).

Modeling and analysis

We used a simulation model developed for the Porcupine caribou herd (Kremsater, 1991; Russell, 1991; White, 1991) to generate the following relations: (1) recruitment of calves to yearling age-class as a function of adult-female body fat (percentage of live body weight) in the preceding fall; (2) N_{max} as a function of N_f and recruitment of calves to yearling age-class; and (3) N_{max} as a function of N_f and adult-female body fat in the preceding fall. The model is a deterministic model based on many years of study of the Porcupine caribou herd. It calculates body condition and growth rates of individual animals as a function of food resources and energy expenditures in its ENERGY submodel. It calculates population demographics and dynamics as a function of energy balance and body condition of individual animals in its POPULATION submodel. The model has been developed specifically for the Porcupine caribou herd and incorporates average values of all variables for that herd and its habitat. Therefore, model predictions for our harvest-threshold relations are for best-approximation, "average" conditions. The model is the core of an ongoing research program and so will be subject to refinement for years to come. Harvest-threshold relations can always be recalculated, however, after future changes in the model.

Relation between recruitment of calves to yearling-age class as a function of adult-female body fat in the preceding fall was generated by varying adult-female body fat, throughout its range of reasonable values, as an input variable in the POPULATION submodel, and calculating resultant recruitment the following year (calves to age 12 months). Relations between N_{max} and N_f, N_{max} and recruitment, and N_{max} and both N_f and recruitment were generated, similarly, by varying each of the independent variables throughout its range of reasonable values and calculating the resultant value of N_{max}. Harvest threshold relation of N_{max} as a function of N_f and adult-female body fat was calculated by substituting the relation for recruitment as a function of female body fat into the relation for N_{max} as a function of N_f and recruitment.

Results

Recruitment of calves to yearling age-class was a linear function of adult-female body fat in the preceding fall (Fig. 1a). N_{max} increased linearly with N_f (Fig. 1b) and curvilinearly with both fall fat weight (Fig. 1c) and recruitment (Fig. 1d). The combined response surface (Fig. 2a) indicates that when a havestable surplus exists (i.e., N_{max}>0) N_{max} is lowest at low population levels combined with low rates of recruitment. The population would be most sensitive to hunting when in this area of the response surface.

The harvest threshold relation of N_{max} as a function of N_f and adult-female body fat (Fig. 2b) looks very similar to the response surface of Fig. 2a. However, with adult-female body fat substituted for recruitment, N_{max} now can be calculated as a function of two variables that can be monitored routinely and effectively. The relations are the same as for recruitment: Hunting is most likely to have significant, destabilizing consequences when the population level is low and, especially, when adult females are, on average, in poor body condition (low body fat). Hunting is most likely to be relatively insignificant in reducing the herd when the

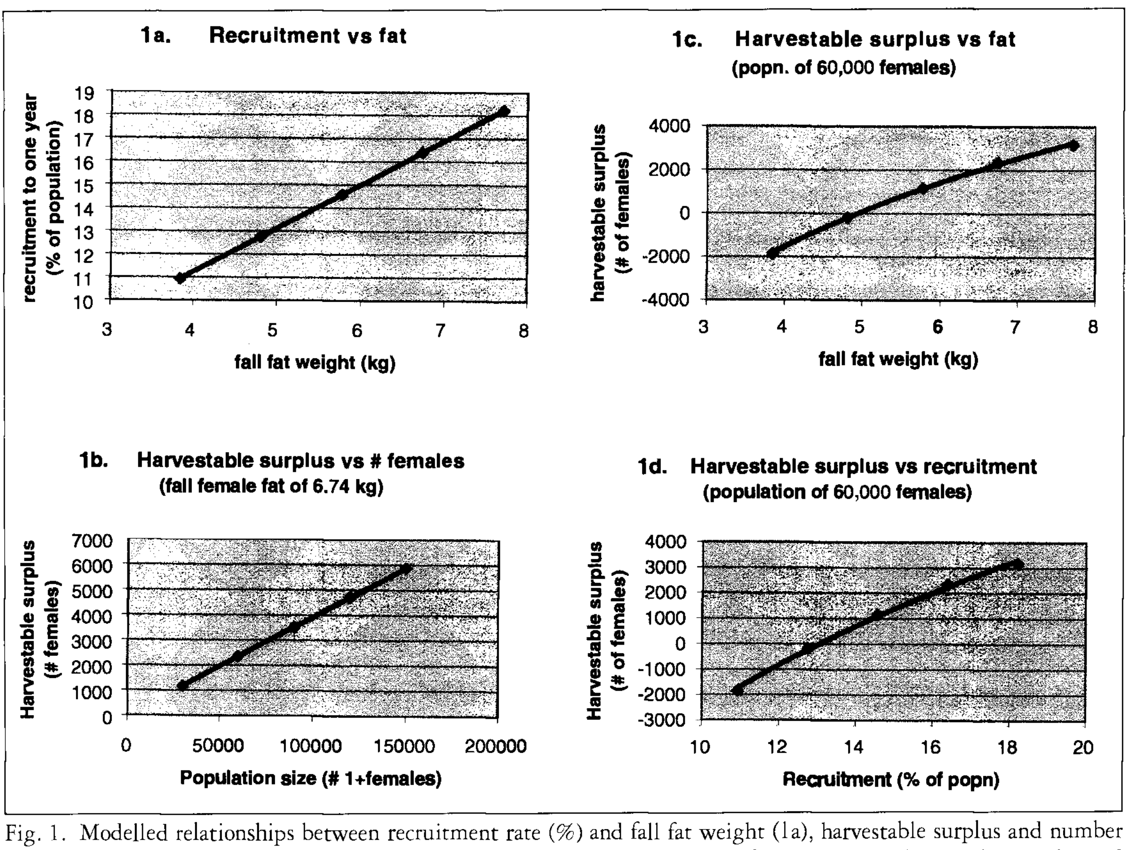

Fig. 1. Modelled relationships between recruitment rate (%) and fall fat weight (1a), harvestable surplus and number of females in population (1b), harvestable surplus and fall fat weight of females (1c) and harvestable surplus and recruitment rate (1d).

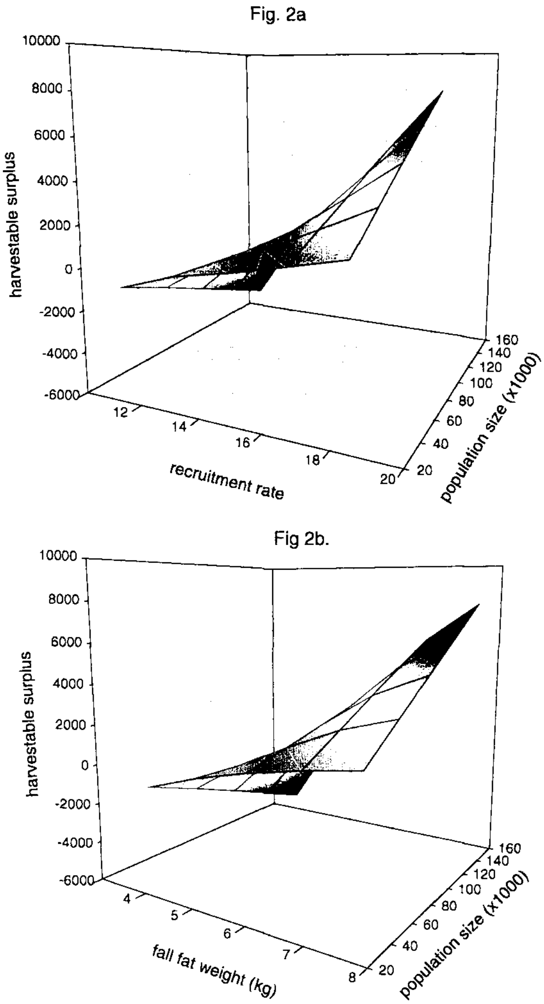

Fig. 2. Modelled response surface relating harvestable surplus and female population size to recruitment (2a) and fall fat levels (2b).

population level is high and adult females are in good body condition (high body fat). The situation of low population level and high body fat would occur when the herd is recovering rapidly from low population levels (e.g., a catastrophic winter die-off). Reduced hunting pressure at such a time would be expected to permit the herd to increase more rapidly than under higher hunting pressure, and relative effects of hunting would be lessened (with higher N_f) in the near future. Conversely, the situation of high population level with low body fat would signal that the herd is in a precarious state - possibly a case of having exceeded the carrying capacity (i.e., a state of density-dependent population limitation) or a case of environmental change in habitat reducing its quality for caribou. This situation is complicated, because the appropriate harvest-management strategy could be very different, depending on the cause(s) of the poor body condition.

Since body fat monitoring of the Porcupine caribou herd was initiated in the mid 1980s, average autumn body fat has been about 6.8 kg (unpubl.). From Fig. 2b and assuming an average female population size for the Porcupine herd of 60 000 animals, we determine the average annual harvestable surplus for the herd would be 2000 females. Average annual harvest of the Porcupine herd during the last decade has been about 2800 animals with about 50% (1400) being adult females (Porcupine Caribou Management Board, 1998). The theoretical maximum harvest was never exceeded during this period.

Discussion

Implications

The harvest threshold relation of N_{max} is a highly simplified concept, calculated from a deterministic simulation model for average conditions. N_{max} should never be regarded as a precise, absolute number. Both adult survival and recruitment actually vary substantially from year-to-year (Fancy *et al.,* 1994), and average conditions seldom prevail. Nevertheless, the shape of the N_{max} response surface is instructive in understanding the dynamics of herd sensitivity to hunting. Actual harvest in relation to N_{max} provides an index of potential magnitude of effect of hunting during any given year. It is very difficult to restrict hunting, however, especially where subsistence needs are great. Thus, co-management of caribou does not react on an annual basis to new data; it reacts to major trends over periods of years (Urquhart, 1996). However, for it to react appropriately at all, it needs practical information (data) and practical guidelines. Periodic monitoring of number of adult females in the population and annual body condition in autumn, combined with herd harvest data and the harvest threshold relation of N_{max}, will provide insightful data for identifying trends and understanding their significance.

One practical implication of instituting such a monitoring system is that hunter attention is immediately focused on importance of the productive component of the population (adult females) and importance of recruitment to the population (calf production and survival). Implications of harvest sex- and age-ratios, therefore, clearly favor harvest of adult bulls during any time of potential herd sensitivity to hunting. This has significant educational value. Furthermore, times of increased sensitivity can be anticipated through the relation of actual (or projected) harvest to N_{max}.

Hunters are always limited in their ability to judge total herd size, because each can see only a small part of it. They, therefore, need to rely on government managers for aerial census data. Government managers, on the other hand, need to rely on hunters for body-fat data. The system encourages (indeed, requires) frequent, meaningful interaction between users and managers working in concert to monitor size and health of the herd and predict its relative sensitivity to hunting. Value of the monitoring system increases with time, because (1) time is required to see real trends through apparent annual variations, (2) time is required to increase familiarity and instill confidence in both the system and cooperation between users and managers, and (3) time is required to build a data base that provides historic perspective and credibility.

"Good times" of increasing herd size and minor or insignificant effects of hunting, such as have prevailed for the past couple decades in the Porcupine herd (Fancy *et al.,* 1994), are easy times for co-management. Management decisions then have little consequence on herd dynamics, so contention is relatively low. However, during periods of population decline, management decisions will be contentious. The test of co-management effectiveness for the Porcupine caribou herd is yet to come. The sooner a monitoring system can be implemented, the better it will be in developing historical perspective and familiarity with users and managers.

Limitations

The harvest threshold relation of N_{max} will prove to be inadequately simple under circumstances that diverge from its underlying, fundamental assumptions. One example is the case where non-human predation of the population increases significantly, such as might be the case under suddenly low population levels (after a major herd decline). This would be a violation of the assumed "average" conditions that went into calculating N_{max} production surplus, where non-hunting mortality has exceeded average conditions. In such a case, increased predation must be considered as additive to hunter harvest. In other words, for a given N_{max}, hunter harvest must be reduced by increased non-human predation on a one-for-one basis. The harvest threshold relation still would be useful, but interpretation of N_{max} in terms of hunter harvest would require additional biological consideration to account for effects of increased predation. It also would require additional kinds of data to quantify the increase in predation.

Another, possibly more likely, complication would arise if the population enters a period of density-dependent population limitation, such as when overgrazing has reduced supply of food. The combination of high population density and low body fat would be the same as for the situation of sudden environmental change (not density-dependent) in reduced habitat quality for the herd. In the first case, hunting of adult females and calves should be increased (even though the N_{max} relation would indicate the opposite), because the objective would be to intentionally reduce population level of the herd. In the second case, the preferred management decision might be to protect females and calves until more is learned about the cause of loss of body condition. In either case, however, additional biological consideration and additional kinds of data would be required beyond the simple N_{max} harvest threshold relation. In both cases, historic perspective from an established monitoring system would be invaluable.

Implementation

Implementation requires that managers and users agree on need and value of a monitoring system. It also requires faithful adherence to data collection. Data requirements are the following: (1) periodic aerial census of population levels, specifically number of adult females; (2) annual sampling of adult-female body-fat indices from a sufficient number of animals for reliable estimate of population mean; and (3) annual tracking of hunter harvest. Hunter harvest data, however, are not required for monitoring size and health of the herd; they merely provide historic perspective and basis for evaluating harvest in relation to herd size and health in any given year. The co-management board would benefit from harvest data in any deliberations about need to change harvest numbers or composition.

Hunters cannot estimate total body fat of caribou directly. Rather, they must measure indices of body fat, which then can be used to calculate body fat. Three relatively simple indices can be obtained from hunter-killed animals without any need to destroy meat or ensure special handling procedures: (1) chest girth, measured with a tape measure, (2) backfat thickness, measured with a ruler, and (3) femur marrow-fat weight or percentage, measured in the laboratory from the femur bone saved by the hunter (Chan-McLeod *et al.,* 1995). All measures should be made in autumn, preferably September or early October. Backfat thickness is a good predictor when body fat exceeds 8%, while femur marrow fat is a good predictor for body-fat levels <9%. Large sample sizes can be obtained by hunters, thereby yielding a relatively precise estimate of the population mean. A starting point for this sort of sampling might be along the Dempster Highway, where hundreds of cows usually are taken by hunters in October each year.

Communication between managers and hunters and between villages is crucial to the successful implementation of any monitoring system to be used in co-management. Data must be easily updated and readily available to all interested parties. That requirement has been virtually impossible until recently. With the advent of the internet, it has now become a relatively simple matter to provide a website where data can be input and/or viewed from any village or government agency at any time. Most villages within the range of the Porcupine caribou herd currently have internet access, and plans exist to expand service to all villages. Users may share information about current location and movements of the caribou herd. Data may be input and managed in any way preferred by users, managers, and the co-management board. Results of analysis of the data, along with the historic data base (or trend summary) may be readily available and viewed by anyone at any time. Political considerations about what data any particular village is willing to share with the "outside" are probably the greatest obstacles remaining. Such nontechnical issues need to be worked out among users and the co-management board.

Implementation of a relatively simple yet effective monitoring system should bring users and managers together in a mutually beneficial relationship of understanding and managing their caribou herd. With increased familiarity and trust in the system, the co-management board is most likely to be able to succeed in recognizing any need for change in management strategies and for accomplishing such change through voluntary participation of remote users. This is a first step along that path.

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