

# Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics

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**Abstract** Conservation strategies for populations of woodland caribou *Rangifer tarandus caribou* frequently emphasize the importance of predator–prey relationships and the availability of lichen-rich late seral forests, yet the importance of summer diet and forage availability to woodland caribou survival is poorly understood. In a recent article, Wittmer et al. (*Can J Zool* 83:407–418, 2005b) concluded that woodland caribou in British Columbia were declining as a consequence of increased predation that was facilitated by habitat alteration. Their conclusion is consistent with the findings of other authors who have suggested that predation is the most important proximal factor limiting woodland caribou populations (Bergerud and Elliot in *Can J Zool* 64:1515–1529, 1986; Edmonds in *Can J Zool* 66:817–826, 1988; Rettie and Messier in *Can J Zool* 76:251–259, 1998; Hayes et al. in *Wildl Monogr* 152:1–35, 2003). Wittmer et al. (*Can J Zool* 83:407–418, 2005b)

presented three alternative, contrasting hypotheses for caribou decline that differed in terms of predicted differences in instantaneous rates of increase, pregnancy rates, causes of mortality, and seasonal vulnerability to mortality (Table 1, p 258). These authors rejected the hypotheses that food or an interaction between food and predation was responsible for observed declines in caribou populations; however, the use of pregnancy rate, mortality season and cause of mortality to contrast the alternative hypotheses is problematic. We argue here that the data employed in their study were insufficient to properly evaluate a predation-sensitive foraging hypothesis for caribou decline. Empirical data on seasonal forage availability and quality and plane of nutrition of caribou would be required to test the competing hypotheses. We suggest that methodological limitations in studies of woodland caribou population dynamics prohibit proper evaluation of the mechanism of caribou population declines and fail to elucidate potential interactions between top-down and bottom-up effects on populations.

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## Introduction

Any evaluation of top-down and bottom-up effects in large ungulates requires information on a broad range of factors, including demographic data, predation rates, range condition, and forage requirements. Predation is expected to exert a powerful influence on prey populations over evolutionary time (Lima and Dill 1990) and may be particularly important for prey populations that incur high neonatal losses due to predation, such as caribou (Adams et al.

1995a). However, even if a prey population is regulated by predation, the habitat and space use patterns of prey that reduce predation risk can negatively affect range quality and increase competition for food (Ferguson et al. 1988; Kotler et al. 1994). Studies that are focused on trophic interactions, as opposed to individual species conservation, emphasize that top-down and bottom-up forces act simultaneously on populations and suggest that dichotomies between the two forms of regulation are largely artificial (Leibold 1989; Hunter and Price 1992; Menge 1992).

Woodland caribou (*Rangifer tarandus caribou*) is a species of conservation status in the boreal forest of North America, and considerable research has emphasized the importance of predator–prey relationships and anthropogenic disturbance to population declines (Kinley and Apps 2001; McLoughlin et al. 2003; Wittmer et al. 2005a, b). Wittmer et al. (2005b) examined the role of top-down and bottom-up factors in the decline of woodland caribou populations in British Columbia by contrasting three alternative hypotheses in terms of predicted differences in instantaneous rates of increase, pregnancy rates, causes of mortality, and seasonal vulnerability to mortality. We suggest that the use of population parameters and mortality factors to assess limiting factors may mask seasonal nutritional deficiencies and has limited value for testing hypotheses for bottom-up effects on ungulate populations. A better synthesis is needed of the relative roles of different ecological factors in affecting population change in woodland caribou. Our objectives in this paper are to encourage researchers to address the interaction between top-down and bottom-up limiting factors when evaluating factors influencing population dynamics. Further, we highlight the importance of detailed nutritional studies, particularly as related to calf viability and survival, when evaluating factors influencing the dynamics of populations in natural conditions.

### Definitions of nutrition-related terms

We define several nutrition-related terms to avoid any ambiguity in terminology. First, “nutrition” was defined by Harder and Kirkpatrick (1994) as the “rate of ingestion of assimilable energy and nutrients”. Second, “nutritional condition” was defined by Harder and Kirkpatrick (1994) as the “state of body components controlled by nutrition and which, in turn, influence an animal’s fitness”. In practice, measures of nutritional condition frequently involved fat or energy stores in the body (Harder and Kirkpatrick 1994). Many different approaches involving the application of a variety of fat indices (e.g., kidney fat, femur fat, weight) have been used to measure nutritional condition: some of these are valuable, whereas others are unreliable (Harder and Kirkpatrick 1994; Cook et al. 2001a).

Both “plane of nutrition” and “nutritional status” are intended to be equivalent. Following Cook (2002), we define both as the level of intake of assimilable nutrients in relation to the daily nutrient requirements of the animal, independent of the animal’s nutritional condition. The energy in food available to the animal is referred to here as digestible energy (DE). Within DE, energy not lost to urine and methane production in the rumen is referred to as metabolizable energy (ME).

### Nutritional effects in ungulates and calf recruitment

For their food regulation and predation-sensitive foraging hypotheses, Wittmer et al. (2005b) assumed that food resources were more limited in winter, an assumption based on the almost exclusive use of arboreal lichens by caribou in the region during winter (Rominger and Oldemeyer 1990). Adult mortality was predicted to be greater in winter for both of these hypotheses and due primarily to malnutrition in the food regulation hypothesis and predation in the predation-sensitive foraging hypothesis. We are concerned that Wittmer et al.’s (2005b) models overlook two important factors: (1) the importance of calf recruitment to population declines of woodland caribou; (2) the absence of nutritional studies demonstrating that food resources in the winter are more limiting than those in the summer in affecting survival.

Wittmer et al. (2005a, b) suggested that recruitment had a minor effect on the observed low rates of population increase because variations in population growth rates among subpopulations were not explained by the observed variations in recruitment (measured from the number of calves at age 9–10 months present during population censuses). The authors did not find a correlation between calf recruitment and  $\lambda$  (finite rate of increase), but they did find a significant correlation between  $\lambda$  and annual survival rates of adult females. Clearly, the rate of increase in a population is a function of both survival and recruitment, and the lack of correlation between  $\lambda$  and recruitment could simply result from consistently low recruitment among subpopulations of mountain caribou. Declining woodland caribou populations are frequently characterized by low recruitment (<12% calves as measured during aerial population surveys) and marginal to high adult survival (>70%) (Bergerud and Elliot 1986; Edmonds 1988; Schaefer et al. 1999; Courtois 2003; McLoughlin et al. 2003). Recruitment may increase to greater than 16% in areas where wolves are experimentally removed (Bergerud and Elliot 1986; Hayes et al. 2003). We note that eight of the 17 subpopulations of caribou described by Wittmer et al. (2005a) had a mean of less than 12% calves during multi-year late-winter population censuses. The importance of low recruitment to population declines of woodland caribou in British Columbia

should not be dismissed. Hayes et al. (2003) examined the effects of wolf reduction on one of three woodland caribou herd ranges in the Yukon and found that although wolf predation strongly limited recruitment of caribou, adult survival did not improve when wolf numbers were reduced. Skogland (1986) suggested that food limitation operated primarily through neonatal losses rather than maternal mortality for wild reindeer herds in Norway.

Predation on calves has been identified as an important cause of low recruitment in woodland caribou (Bergerud and Elliot 1986; Rettie and Messier 1998; McLoughlin et al. 2003); however, we suggest that the methodologies employed in these studies do not account for potential effects of nutrition on calf viability or susceptibility to predation. Evidence from other ungulates suggests that nutrition can and does exert a powerful influence on calf growth and probability of survival (reviewed by Brown and Mallory 2007). Maternal nutrition in winter/spring may strongly affect survival at or near birthing by inducing low birth weight (Keech et al. 2000). Singer et al. (1997) for elk and Keech et al. (2000) for moose reported significant relations between the birth weight of calves and their survival across the summer in predator-rich environments. For juveniles, high levels of growth require good nutrition, a relation that has been well demonstrated for a variety of ungulate species (Holter and Hayes 1977; Verme and Ozoga 1980a, b; Cook et al. 2004b). Significant relations among summer nutrition, disease, and juvenile mortality have been reported for bighorn sheep (Cook 1990) and mule deer (Tollefson 2007). Further, if low birth weight predisposes to mortality across the summer in predator-rich environments (Singer et al. 1997; Keech et al. 2000), it follows that substantial nutritional deficiencies in the summer also might increase the summer mortality of calves in predator-rich environments, but this hypothesis is largely untested.

We suggest that existing research has not elucidated the relative importance of summer versus winter nutrition to woodland caribou populations. In temperate and arctic regions, large herbivores lose fat in winter and gain fat in summer (Dauphiné 1976; Reimers et al. 1983; Cook et al. 2004b). The amount of energy animals should consume over summer for fat accretion depends both on how much fat they lost during the previous winter and how much fat they will need over the coming winter. During the summer, the energy costs of lactation plus that of recovering from the previous winter weight loss can more than double daily ME requirements compared to those of non-lactating, non-compensating females in the summer/autumn (Cook 2002). The importance of summer nutrition for lactation, calf growth, and weight gain prior to the winter period of weight loss suggests that seasonally available vascular plants may be equally or more important than lichens for successful reproduction (Brown and Mallory 2007). The

summer diet of the caribou is the most diverse of any season, and all major plant groups are eaten, including forbs, graminoids, and leaves of shrubs (Bergerud 1972; Ferguson et al. 1988). Boertje (1990) suggested that an assessment of caribou nutritional status based on lichen abundance was inadequate and recommended a more complete evaluation of diet quality, diet composition, activity, and energy requirement in assessing forage limitations for a particular caribou population. We suggest that the effects of summer range on the body condition of caribou at the onset of winter may be equally or more important than the effect of winter range conditions on winter survival.

### Pregnancy rate as an indicator of nutritional influences

In a review of the population dynamics of large herbivores, Gaillard et al. (2000) suggested that adult fecundity of most large herbivores is resilient to a wide range of environmental conditions. Skogland (1986) suggested that the fecundity of migratory populations may be less sensitive to environmental variation than sedentary populations (e.g., woodland caribou). Although pregnancy rates can vary in relation to population density (Gaillard et al. 2000), the results of a number of published studies suggest that pregnancy rate may not be an effective indicator of nutritional influences in many settings and that it has limited value in contrasting competing hypotheses of population decline in ungulates (Gerhart et al. 1997a; Cook et al. 2004b). In *Rangifer* populations, summer nutrition has been found to be an important determinant of pregnancy rate, whereas winter nutrition may be more influential in parturition rates and calving dates (Skogland 1983; Couturier et al. 1990; Cameron et al. 1993). As a result, a herd may be nutritionally stressed in winter and still have high pregnancy rates. Wittmer et al. (2005b) measured caribou densities relative to the area of forests >140 years of age because these caribou are obligate arboreal lichen feeders in winter and arboreal lichens are most abundant in that forest type. As a result, a higher density of caribou on the winter range could conceivably result in higher pregnancy rates due to the early loss of calves and early dates of weaning improving the summer nutrition of any particular female and, therefore, the probability of conception in autumn.

Caribou that extend lactation into the late autumn are less likely to be pregnant than those that cease lactation earlier (Gerhart et al. 1997a). Escaping the nutritional demands of lactation over substantial portions of the summer–autumn lactation period enhances fat accretion in late summer and/or autumn and increases the chances that cows will successfully breed (Cook et al. 2004a). Nonlactating females are generally common in herds that have low rates of neonatal survival and, consequently, pregnancy rates are

usually high (Gerhart et al. 1997b; Skogland 1991). Where predation on juveniles during the summer is high, as is reported for woodland caribou (Crête and Desrosiers 1995; Gustine et al. 2006), the release from the nutritional demands of lactation will increase herd-level pregnancy rates. As a result, predation can mask or hide the effects of nutrition on the herd, if pregnancy rates are used as an index of food limitation.

Summer nutritional deficiencies can have important limiting effects on herds without nutrition having an apparent effect on pregnancy rate. Recruitment could remain low if forage resources in summer are insufficient to allow lactating females to both provide adequate milk and recover endogenous energy reserves prior to the breeding season (Gerhart et al. 1997b). Gerhart et al. (1997b) demonstrated that using pregnancy rates or parturition rates of random samples of a herd may underestimate the importance of nutrition and recommended using samples of lactating females. Cook et al. (2004b) found that calf and yearling growth and development, adult body fat accretion rates, and timing of breeding were better indicators of summer/autumn nutritional stress in captive elk than breeding probability of adult lactators or probability of winter starvation (Table 1). It is reasonable to suggest that similar indices are appropriate for other ungulates, such as caribou. The indicators listed in Table 1 are unlikely to be detected in most telemetry-based studies of wild populations, or at least their relations to summer nutrition would be undetectable. In short, real nutrition studies are needed to fully understand the influence of nutrition.

### Seasonal risk of mortality

In the predation hypothesis, Wittmer et al. (2005b) predicted that predation would be greater in summer due to the

greater range overlap with wolves and moose during that season. We suggest that this prediction is complicated by the large-scale habitat selection patterns of mountain caribou that affect forage availability and predation risk. Mountain caribou in British Columbia typically occupy higher elevation alpine habitats in late winter, move to lower elevations in spring to access newly emerging green vegetation, then return to higher elevations for the calving period and summer (Apps et al. 2001; Wittmer et al. 2006). Wittmer et al. (2005b) found that adult mortality from predation was highest during calving and the summer, and the authors interpreted the high summer mortality as supporting evidence for the predation hypothesis. We argue that the high adult mortality during the calving period, when females are hypothesized to move to areas with naturally low densities of predators as an anti-predator strategy (Bergerud et al. 1984), suggests we do not yet fully understand the adaptive significance of seasonal movement patterns in woodland caribou.

In a study of calf survival of woodland caribou in British Columbia, Gustine et al. (2006) found that parturient woodland caribou selected calving areas with greater vegetative change (index of nutritional value associated with spring growth) – at the expense of greater predation risk. Plants in early phenological stages are highly nutritious and digestible (Albon and Langvatn 1992), and it is possible that the return to higher elevations during calving reflects the altitudinal gradient in plant emergence in relation to snowmelt. Albon and Langvatn (1992) found that variations in the body weights of red deer were significantly related to the crude protein level in the vegetation available during the summer and that the migration was timed in relation to snowmelt to exploit the maximal protein concentrations at higher altitudes. Wittmer et al. (2006) speculated that seasonal shifts in limiting factors from predation to food might affect caribou movement behavior. Potential interactions

**Table 1** Indicators of summer/autumn nutritional stress for elk (based on Cook et al. 2004b)

Indicator	Sensitivity	Threshold for decline (DE in summer forage)
Probability of winter starvation	Variable <sup>a</sup>	Linear with/out thresholds
Calf and yearling growth and development	High	3–3.2 kcal/g
Yearling breeding probability (age of primiparity)	High	3–3.2 kcal/g
Adult body fat accretion rates	High	2.85 kcal/g
Timing of adult breeding	High	2.8–2.85 kcal/g
Timing of birthing	Moderate <sup>b</sup>	2.8–2.85 kcal/g
Breeding probability of adult lactators	Moderate	2.65–2.7 kcal/g

DE, Digestible energy

<sup>a</sup> Dependent on winter severity and age class in addition to summer nutrition and autumn body fat levels

<sup>b</sup> Strong delays in breeding can translate to delays in birthing, but the effect may be modified by weather and nutrition in winter and spring

between top-down and bottom-up factors should not be dismissed for woodland caribou populations in British Columbia.

### Cause of mortality

Estimates of mortality factors, based on collared animal remains, may be biased towards more obvious proximal cues. The relative importance of different mortality factors is often based on the sample of identifiable causes, with unknown causes possibly accounting for a high percentage of mortalities. Evidence of predation (e.g., disarticulation, crushed bones, puncture wounds) is likely more easily discernible than nutritional deficiency in examination of animal remains and may result in the biased clumping of nutrition-related mortality into the category of “unknown cause”.

Wittmer et al. (2005a, b) attempted to identify evidence of malnutrition in collared animal mortalities (where carcass condition permitted) based on measures of bone marrow, visceral, and rump fat deposits. Details of the methodology used for calculating the nutritional condition indices were not provided, and we suggest that caution is warranted in the interpretation of such data, depending on the model employed. Cook et al. (2001a, b) identified differences among body condition index models in the approach they adopted to predict nutritional condition of captive elk under controlled dietary conditions. Although measures of rump fat are of value for assessing the nutritional condition in live animals, Cook et al. (2001a) recommended using a modified Kistner score for dead animals. The Kistner system includes scoring based on fat in indicator depot sites (cardiac, omental, perirenal, and subcutaneous areas) and the condition of the skeletal muscle mass (Kistner et al. 1980). Notably, the authors identified limitations to the use of femur marrow fat as an index of nutritional condition. Femur marrow fat only varied in relation to nutritional condition in elk under poor conditions (when body fat was below 6%), but it had no predictive power for moderate to high levels of nutritional condition (Cook et al. 2001a). Bone marrow fat is one of the last body stores of fat to be used, and low values of marrow fat tend to be representative of acute nutritional deprivation (Dauphiné 1971; Mech and DelGiudice 1985; Harder and Kirkpatrick 1994). As a result, an animal could have used most of its total body fat and still have almost all of its marrow fat. Further, moderate reductions in nutritional condition can have significant effects on overwinter survival in wild ungulates (Cook et al. 2004b).

The examination of collared animal remains, particularly adults, does not address the causes of early calf mortality. Whitten et al. (1992) concluded that calf mortality could be underestimated using only radio-collared calf data due to

the high incidence of mortality within 48 h of birth – before calves can generally be collared. In a study of early calf survival in the Porcupine herd of barren-ground caribou *R. t. granti*, Whitten et al. (1992) found that predation was an important cause of death in radio-collared calves older than 48 h; however, most mortality (59–74%) of calves born to radio-collared females occurred within 48 h of birth. Many of these deaths were attributed to stillbirths, defects, or low birth weights. Similar studies have not been conducted to address the causes of mortality within 48 h of birth for sedentary woodland caribou populations.

Finally, the identifiable causes of mortality may suggest the importance of proximally limiting factors, but they do not take into account possible interactions that affect vulnerability to mortality. Interactions among mortality factors may occur, and nutritional condition has been shown to predispose animals to predation (Pimlott et al. 1969; Keith et al. 1984). Similar to studies of boreal and mountain woodland caribou (Rettie and Messier 1998; Kinley and Apps 2001; McLoughlin et al. 2003), Hearn et al. (1990) reported that predation was the most common cause of death for members of the George River herd (forest-tundra population) between 1983 and 1987 – yet this herd is believed to be regulated by summer nutrition (Crête and Huot 1993). The similarity in documented mortality factors for herds with a different relative importance of top-down and bottom-up factors highlights the need to evaluate multiple explanatory factors with empirical data.

### Inferences drawn from population parameters

Limiting factors of woodland caribou populations are frequently inferred from an assessment of population parameters, and inferences are made in relation to either top-down or bottom-up forces (Bergerud and Elliot 1986; Edmonds 1988; Crête and Desrosiers 1995; Rettie and Messier 1998; Kinley and Apps 2001; Hayes et al. 2003; McLoughlin et al. 2003). Predator limitation is often inferred from high pregnancy or parturition rates, good body condition, and low recruitment or high adult mortality. A fundamental problem with this approach is that dependent variables, such as recruitment rate or pregnancy rates, are used to explain ecological interactions without the proper quantification of the assumed causative factors (i.e., independent variables). As a result, it becomes difficult to assess the relative explanatory power or potential interactions of top-down and bottom-up forces in relation to trends in population change. Regarding top-down or bottom-up mechanisms, Tveraa et al. (2007) showed that the quality of the winter ranges influenced whether a population was subject to top-down or bottom-up mechanisms. There seems to be no simple answer to this problem, and behavior, like migration,

may complicate further the relative importance of summer and winter grazing ranges.

There is a general consensus that predation acts to reduce the importance of forage as a limiting factor in woodland caribou by holding populations at densities lower than the carrying capacities defined by absolute food abundance (Ahti and Hepburn 1967; Bergerud 1974; Thomas and Gray 2002). Although predation can limit the population growth rate (Bergerud and Elliot 1986; Hayes et al. 2003) and hold caribou populations at low densities (Crête and Manseau 1996), Boertje (1990) suggested that conditions of nutrition limitation can be expected to occur over a wide range of caribou densities due to the range of factors that can influence nutrition. In this context, a few recent papers have focused on the different vegetation states created by (over) grazing by herbivores – see, for example, van der Wal (2006) and Olofsson (2006) – which can alter the carrying capacity of an area. Thus, nutrition limitation can occur at different densities and change the relative importance of summer versus winter grazing ranges. Even if predation holds a caribou population below the carrying capacity defined by food, the absolute availability of food may be less constraining to fitness than the quality of forage (Parker et al. 1999; Cook 2002). The quality of forage in many ecosystems depends to a large degree on long-term climate conditions, variations in seasonal weather patterns, soil type, disturbance regimes, and other factors, and considerable variation very well may exist in forage quality levels available to foraging herbivores (Verme 1969; Cook 2002). In a controlled investigation of 57 captive adult female elk, Cook et al. (2004b) demonstrated that the over-winter survival of calves was sensitive to small (10–20%) differences in the digestible energy content of food that they consumed in summer. Such subtle changes in the plane of nutrition would not be apparent from data on the causes of caribou mortality or mortality season.

### Concluding remarks

We do not contest that predation has a major effect on woodland caribou behavior and population change. The findings of Wittmer et al. (2005b) for rate of population increase in relation to population density in British Columbia woodland caribou are consistent with the predation hypothesis. However, evidence of predator limitation should not imply that food availability or quality does not affect caribou population dynamics. Growing evidence on other taxa suggests that both top-down and bottom-up forces affect natural herbivore populations and that interaction effects may occur among limiting factors. Vegetation can affect herbivores directly by influencing their performance and survival, and indirectly by mediating the effects

of predators on herbivore populations (Gratton and Denno 2003; Jiang and Morin 2005). Research conducted on caribou in Denali National Park, Alaska, suggests the importance of climate and nutrition to caribou populations that exhibit low recruitment due to predation (Adams et al. 1995a, b, Adams 2005).

Apart from body condition indices from collared animal remains, limited information was available on the nutritional status, forage quality or availability, calving dates, neonatal viability, age of primiparity, or causes of calf mortality for the woodland caribou populations studied by Wittmer et al. (2005b). We find the lack of such information problematic where competing hypotheses are employed to evaluate the importance of top-down and bottom-up factors to caribou population dynamics. Even if predator densities or predator-induced mortality rates are high for a caribou population, assessing the importance of food cannot be accomplished without a careful examination of caribou foraging behavior and nutrient budgets. Empirical studies of other *Rangifer* spp. indicate that nutrition, growth, productivity, and survival are closely linked, and the simultaneous importance of food and predators has been demonstrated for other predator–prey systems.

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