Habitat Influences on Woodland Caribou Populations in Canada: A New Research Direction

September 6, 2007

Katherine Parker, University of Northern British Columbia, Prince George, B.C.

Perry Barboza, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK

John and Rachel Cook, National Council for Air and Stream Improvement, La Grande, OR

Darren Sleep, National Council for Air and Stream Improvement, Montreal, Quebec

Introduction

Caribou populations are experiencing increased anthropogenic disturbances and greater climatic variability throughout the circumpolar north. In Canada, woodland caribou have disappeared from southern ranges and are declining on other ranges where they presently occur. Four populations of woodland caribou are listed as "endangered" (1), "threatened" (2), or "special concern" (1) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the Federal Species at Risk Act. Field research indicates that past declines resulted from complex interactions among human disturbances, habitat change, and predator-prey relationships. In the future, woodland caribou face accumulating challenges from growing human populations and potential changes in climate. A progressive change towards mild winters and longer and warmer summers may greatly alter habitat and other environmental conditions for caribou, particularly if catastrophic wildfire regimes are elevated. Thus, threats to woodland caribou populations increasingly may involve changes in the quality and availability of habitat.

The scientific literature describing the role of habitat in woodland caribou populations in Canada is remarkably underdeveloped. Relationships between caribou and their predators are better studied, but those relations may be indirectly influenced by habitat and nutritional value of the caribou's food supplies. Compelling evidence from around the globe documents the direct influence of nutrition on a variety of demographic attributes of large ungulates (hooved mammals), including barren-ground caribou. In other words, nutrition may influence the resilience of large ungulate populations to predation or can, by itself, regulate or limit size and growth rates of ungulate populations. Even so, studies that define the effects of habitat change on nutrition, and nutrition's effects on woodland caribou across Canada have been[1] and currently remain[2] largely non-existent. Therefore, increasing the depth and breadth of scientific information on the role of habitat in sustaining caribou populations will improve conservation programs. It also will elevate our ability to forecast woodland caribou responses to future threats from changes in climate, ecosystems, and disturbance regimes.

The forest products industry has a considerable stake in the management of woodland caribou populations and habitat across Canada. Recent publications contend that forest management and viability of woodland caribou may be fundamentally incompatible [3], and predation research suggests that certain forest management strategies may enhance predation, with catastrophic consequences to caribou[4]. Unfortunately, this research has provided only rudimentary insight about how changing habitat might

[1] NCASI. 2007. A review of ungulate nutrition and the role of top-down and bottom-up forces in woodland caribou population dynamics. Technical Bulletin No. 934, NCASI, Research Triangle Park, North Carolina, USA.
[2] NCASI. 2007. State of knowledge and analysis of current research on woodland caribou in Canada. Technical Bulletin No. 939, Research Triangle Park, North Carolina, USA.
[3] Vors et al (2007, J. Wildl. Manage. 71(4): 1249-1256), Schaefer and Mahoney (2007, J. Wildl. Manage. 71(6):1753-1757).
[4] Wittmer et al (2005, Oecologia, 144:257-267)

affect caribou, particularly across a variety of ecological-climatological settings. Moreover, forest management offers a considerable array of habitat treatment options that can produce a variety of forest vegetative conditions. Woodland caribou studies have not evaluated the possibility that certain forest management strategies might have benign effects, and that others might have beneficial effects. For example, moderate overstory thinning, or small patch cuts widely distributed across landscapes, might improve the diversity and abundance of preferred vascular plants used by caribou on spring through autumn ranges, without appreciably reducing lichen availability or inducing colonization or substantial increases of moose and wolf populations. Careful research is needed to identify ways to enhance compatibility of forestry and viable woodland caribou populations. It will have to (1) delve heavily into fundamental and basic relations of habitat and population responses, because understanding how these operate is crucial for identifying ways to improve habitat, and will have to (2) explicitly evaluate how silviculture might be used to benefit woodland caribou populations.

We propose two overarching, working hypotheses.

(1) Across Canada, the suitability of habitat for woodland caribou undoubtedly varies in relation to broad-scale patterns of climate, soils, topography, vegetation type, successional trajectories, and land use. The influences of habitat on caribou populations undoubtedly vary as well. We hypothesize that at least in some settings, habitat has limiting effects, mild in some areas perhaps ranging to severe in others. There may be potential to benefit caribou by improving habitat in many of these areas via active management.

(2) Judicious forest management may provide valuable opportunities to benefit woodland caribou populations and thus may provide opportunities to the forest products industry to play a positive and proactive stewardship role for woodland caribou. However, building support and credibility for such opportunities requires new and creative research that has not yet been implemented for woodland caribou.

Goal and Objectives

We propose an innovative research program on the relations between woodland caribou and habitat that will define habitat-based limitations to populations and will identify strategies of forest habitat management and landscape-level forest planning that can help sustain caribou populations across Canada. We propose three objectives:

(1) Fill important information gaps on how habitat contributes to performance of woodland caribou populations, with emphasis on nutritional paths of influence. Our emphasis on nutrition reflects two fundamental presumptions: (a) nutritional effects represent the most pervasive *direct* influence of habitat on large herbivore populations in many ecological settings, and (b) nutritional ecology offers a quantitative cause-and-effect basis for describing how habitat changes contribute to future populations. This is important because habitat can be managed to meet conservation goals.

(2) Develop the science necessary for integrating nutritional ecology with other environmental influences to explicitly define contributions of habitat to woodland caribou populations. The science of integrating influences of nutrition with forest vegetation change, predator avoidance, human disturbance, and weather for large herbivores has been remarkably slow to develop. The plight of woodland caribou underscores the need for developing this science.

(3) Provide stringently-tested, forest management and decision-support tools (models) that link habitat attributes to population demographics of woodland caribou. Potential value of this type of population model has been illustrated[5], but widespread application in forest management and planning has been hindered due to an absence of suitable field data for testing. Our data will support extensive testing, and we anticipate that the final nutritionally-based habitat-supply models will help biologists

[5] See Coughenour and Singer for elk (1996, Bien. Conf. Greater Yellowstone Ecosys. 2:169-179); Turner et al. for elk (1993, Ecol. Model. 69:163-184); Moen et al. for moose (1997, Ecology 78:505-521); Hobbs for mule deer (1989, Wildl. Monogr. No. 101). Coughenour and Singer showed these models can successfully track long-term population trajectories and winter survival in Yellowstone. Hobbs showed they can be effective management tools with important practical applications.

understand and forecast how geographic distribution, amount, timing, and type of disturbances interact with a variety of biotic and abiotic features of landscapes to affect caribou populations. Moreover, integrating our research results with forest management planning models that link with other tools such as forest-growth models will enhance their use in the future. This integration will vastly improve relevance of our field studies.

Approach

Our strategy will include a unique integration of classic "animal science" experiments in penned settings with captive caribou, foraging studies with tame caribou in natural plant communities, and monitoring of population attributes and habitat use of wild caribou. This program will require about 12 years to complete, with periodic reviews to refine future directions, conducted in three phases described below.

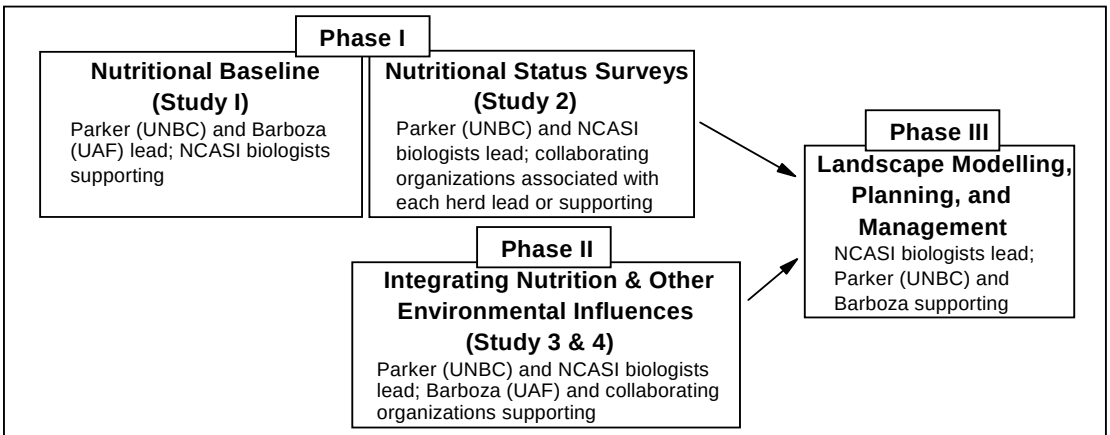

Figure 1. Collaborators leading or supporting the three phases of proposed research to define habitat influences on woodland caribou populations across Canada.

Phase I.-- The purpose of this phase is to build a nutrition information base to support and guide our subsequent field studies. The first study will develop better quantitative understanding of basic nutritional effects on caribou reproduction and survival probability, using tightly controlled experiments. Work will be conducted with hand-reared woodland caribou calves at the R.G. White Large Animal Research Station, Institute of Arctic Biology, University of Alaska-Fairbanks, where reindeer and caribou herds have been maintained for over 20 years. This work will have four objectives:

Objective 1: increase understanding of nutritional requirements and the quantitative implications of nutritional deficiencies on reproductive and survival performance. Focus will be year-round, such that nutritional influences of food quality and quantity on fetal development, lactation, calf growth, breeding dynamics, overwinter survival probability, and carry-over effects across seasons will be evaluated.

Objective 2: identify animal performance "thresholds" useful as evaluation criteria with which to judge nutritional status of wild caribou and nutritional adequacy of their forage (e.g., body fat levels needed for pregnancy and to survive winter; forage nutrient levels to support optimal calf growth). These criteria will be crucial for subsequent field studies.

Objective 3: use the experiments to test and further refine extant caribou nutrition models (primarily Russell's et al. caribou energetics model[6]) of animal performance responses to nutrition. One key aspect of linking nutritional resources to herbivore populations involves quantitative estimates of nutrition's effects on animal performance; these are very difficult to measure accurately in the wild but can be measured under controlled conditions with tractable animals.

[6] Russell, D.E., R.G. White, and C.J. Daniel. 2005. Energetics of the Porcupine Caribou Herd: a computer simulation model. Canadian Wildlife Service, Technical Report Series 141, Ottawa, Ontario, Canada.

Objective 4: rigorously test state-of-the-art techniques to measure nutritional condition (i.e., fat and protein levels) of live, free-ranging caribou[7]. Nutritional condition is a powerful measure of the nutritional adequacy of the herbivore's environment, but has been difficult to measure accurately without sacrificing study animals. This work also will provide equations to enhance comparability of nutritional condition estimates among past studies that used a variety of condition indexing techniques (e.g., kidney fat, rump fat, body condition scores), collected from either live or dead animals.

For the second study, we will conduct a multi-regional "compilation" of nutritional condition indices for caribou, by compiling data in extant literature collected around the globe and by conducting new research surveys for woodland herds in Canada[8]. New research will involve capture of wild caribou under two situations, (a) where we "tag-along" with ongoing research capture operations and (b) where we provide the funding and "lead" the capture operations. These data (with ancillary estimates of pregnancy and survival) will help describe the range in variation of nutritional condition across broad-scale climatic regimes and forest conditions, provide insights into possible nutritional limitations on woodland caribou populations in Canada, and provide guidance for subsequent field research.

Phase II.-- The purpose of this phase of work is to increase understanding of how caribou use various environmental resources to enhance survival and reproduction, and to improve knowledge of how habitats and disturbance regimes can be effectively managed across landscapes on behalf of caribou populations. This work will include two studies conducted at three or four regional sites, selected to represent at least three major vegetative zones that woodland caribou occupy in Canada. The first will evaluate how forest overstory-understory characteristics and specific vegetative disturbance types affect caribou nutrition, at the *level of forest stands*. Particularly using silviculture, we will create study plots of markedly different understory community attributes. We will place our hand-reared, tractable caribou in these study plots (i.e., small enclosures of 1-4 ha) *and* in additional plots placed in the extant communities of each study area, and collect data on what foods they eat, nutritional levels of actual diets, intake rates of digestible energy and protein and time spent foraging[9] as a function of treated and natural, early through late successional forest community types. Three primary objectives include:

Objective 1: evaluate relationships between plant community characteristics and foraging dynamics to better understand how forest communities influence nutritional status of caribou.

Objective 2: develop and investigate explicit silvicultural prescriptions to improve the nutritional environment on native caribou ranges and eliminate to the extent possible any negative influences from timber harvest or other disturbance types.

Objective 3: develop forest stand-level algorithms that relate forest community characteristics to foraging responses of caribou for refinement and testing a foraging component of an energetics and protein balance model (e.g., the Russell et al. model). Basic data would involve foraging efficiency and nutrient acquisition estimates.

The second study of Phase II will evaluate influences of nutritional and other habitat resources on habitat use, distribution, and nutritional condition of wild caribou *at landscape scales*. It will address two related questions involving wild caribou herds at the three regional sites: (1) how do caribou respond to and select from habitat resources, with special focus on nutritional resources available to them at each of the regional sites; and (2) how do the explicit habitat use patterns of each animal influence annual cycles of nutritional condition, reproduction, and survival? This will involve capturing with helicopters the same caribou each spring and fall across years, attaching global-positioning system (GPS) telemetry collars that will provide detailed data of habitat use and activity profiles, and measuring body weight and condition, pregnancy and lactation status at each capture. To the extent possible, the first and this second study will overlap spatially; data from the foraging trials will be used to quantify the nutrition levels that caribou can actually acquire from each forest community type. These nutrition levels will provide for

[7] E.g., see Cook et al., 2001, 2007 (J. Wildl. Manage. 65:973-987, 71:1934-1943).
[8] E.g., see Gustine et al., 2007 (Rangifer Spec. Issue No. 17:65-72) or Cook et al., 2004 (J. Mammal. 85:714-722).
[9] E.g., see Parker et al., 1999 (Wildl. Monographs No. 143).

mapping nutritional resources across forested landscapes in *units demonstrated to be relevant to foraging caribou.* Along with other standard habitat variables (e.g., roads, topography), detailed resource-use statistical analyses will show how caribou use resources available to them at each regional study site.

Phase III.-- We will coalesce our data sets and individual model components developed/refined in earlier work to produce a final forecasting model that can support forest management planning and decisions by managers, planners, researchers, and others. The model will be in the form of "spatially-explicit population models"[10], with utilities to (1) describe current and track future changes in habitat conditions with relevance to caribou, (2) predict distributions and habitat use of woodland caribou based on distributions of nutritional resources and other habitat attributes, (3) simulate nutrient acquisition rates, and balances of energy and protein, (4) simulate animal performance in terms of reproduction and survival, (5) incorporate user-defined direct mortality due to predation and hunting and (6) forecast population trajectories. The purpose of the model will be to forecast the *contributions of habitat* to population dynamics. By offering user-defined estimates of predation and hunting losses, it also potentially will provide a basis for comparing habitat influences versus other factors causing direct mortality. We anticipate the use of relatively new, individual-animal modeling techniques[11] that will build on first-generation models developed for elk, deer, and moose and current energetics models for caribou.

Schedule

Phases I-III will be implemented sequentially, with field work starting with calf capture and rearing in spring 2008 and experiments of Phase I continuing through 2014. We anticipate that the second study of Phase I, developing data sets of nutritional condition of Canadian caribou herds, will begin late in 2008 and continue at least 5-6 years, depending on how opportunities to capture caribou develop. Creating study plots for Phase II foraging experiments will begin in 2008-09, and fieldwork will begin in earnest in 2012 and last for six years. Because some of the same animals will be used, the foraging experiments of Phase II cannot begin until most of the animal science experiments of Phase I are complete. Formal model development for Phase III will begin after data analyses for most of Phase I is completed, about 2014, with prototype models ready for testing as Phase II field work wanes, in about 2018. We expect completion of all work in 2020.

Research Team

We propose a collaborative team approach to this ambitious undertaking to integrate and enable across multiple areas of expertise. Principle investigators have a long history of conducting captive and wild animal research in laboratory and wild settings. Dr. Parker has conducted large ungulate research with focus on bioenergetics and nutrition since the early 1980s, and has conducted research of woodland caribou population dynamics, landscape ecology, and nutrition at UNBC over the last decade. Dr. Barboza is a nutritional physiologist who has worked on several herbivores, including projects on wild and captive caribou and other ungulates at the Institute of Arctic Biology over the last 10 years. NCASI's large ungulate biologists (J. and R. Cook) have conducted large ungulate energetics and nutrition research in the Pacific Northwest for over 15 years, with specific focus on applied nutrition in the context of habitat evaluation, forest succession, and population dynamics in managed forest ecosystems. Dr. Sleep manages NCASI's Canadian forestry program and has experience in statistical modeling and landscape ecology, with a focus on resource selection and behavioural ecology. He has just completed a report on the state of knowledge and analysis of current research on woodland caribou in Canada.

[10] Dunning et al. 1995. Spatially explicit population models: Current forms and future uses. Ecol. Applic. 5:3-11.
[11] Grimm and Railsback. 2005. Individual-based modeling and ecology. Princeton Univ. Press, Princeton, New Jersey, USA.

Relevant literature for Dr. Parker:

Gustine, D.D., K.L. Parker, and D.C. Heard. 2007. Using ultrasound measurements of rump fat to assess nutritional condition of woodland caribou in northern British Columbia, Canada. Rangifer Special Issue No. 17:65-72.

Gustine, D.D., K.L. Parker, R.J. Lay, M.P. Gillingham, and D.C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165:1-32.

Parker, K.L., P.S. Barboza, and T.R. Stephenson. 2005. Protein conservation in female caribou (Rangifer tarandus): effects of diet quality during winter. Journal of Mammalogy 86: 610-622.

Johnson, C.J., K.L. Parker, D.C. Heard, and D.R. Seip. 2004. Movements, foraging habits, and habitat-use strategies of northern woodland caribou: implications for forest practices. Journal of Ecosystem Management 5:22-35.

Parker, K.L. 2003. Advances in the nutritional ecology of cervids at different scales. EcoScience 10:395-411.

Johnson, C.J., N.D. Alexander, R.D. Wheate, and K.L. Parker. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. Forest Ecology and Management 180:241-248.

Johnson, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002. A multi-scale behavioral approach to understanding the movements of woodland caribou. Ecological Applications 12:1840-1860.

Johnson, C.J., K.L. Parker, and D.C. Heard. 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. Oecologia 127:590-602.

Johnson, C.J., K.L. Parker, and D.C. Heard. 2000. Feeding site selection by woodland caribou in northcentral British Columbia. Rangifer Special Issue No. 12:159-172.

Parker, K.L., M.P. Gillingham, T.A. Hanley, and C.T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monographs 143. 48 pp.

Parker, K.L., M.P. Gillingham, and T.A. Hanley. 1993. An accurate technique for estimating forage intake of tractable animals. Canadian Journal of Zoology 71:1462-1465.

Parker, K.L., M.P. Gillingham, T.A. Hanley, and C.T. Robbins. 1993. Seasonal patterns in body weight, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus heminionus sitkensis*) in Alaska. Canadian Journal of Zoology 71:1397-1404.

Parker, K.L., R.G. White, M.P. Gillingham, and D.F. Holleman. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. Canadian Journal of Zoology 68:106-114.

Parker, K.L. 1989. Growth rates and morphological measurements of Porcupine caribou calves. Rangifer 9:9-13.

Relevant literature for Dr. Barboza:

Ihl, C. and P.S. Barboza. 2007. Nutritional value of moss for arctic ruminants: a test with muskoxen. Journal of Wildlife Management 71 (3): 752-758.

Barboza, P.S. and K.L. Parker. 2006. Body protein stores and isotopic indicators of N balance in female reindeer (*Rangifer tarandus*) during winter. Physiological and Biochemical Zoology 79:628-644.

Barboza, P.S., T.C. Peltier and R.J. Forster. 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiological and Biochemical Zoology 79: 497-513.

Knott, K.K., P.S. Barboza, and R.T. Bowyer. 2005. Growth in arctic ungulates: postnatal development and organ maturation in reindeer, caribou and muskoxen. Journal of Mammalogy. 86: 121-130.

Barboza, P.S. and P.E. Reynolds. 2005. Monitoring nutrition of a large grazer: muskoxen on the Arctic Wildlife Refuge. International Congress Series 4663: 327-333

Barboza, P.S., D.W. Hartbauer, W.E. Hauer and J.E. Blake. 2004. Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus tarandus*). Journal of Comparative Physiology B. 174: 309-317.

Barboza, P.S., E.P. Rombach, J.E. Blake and J.A. Nagy. 2003. Copper status of muskoxen: a comparison of wild and captive populations. Journal of Wildlife Diseases 39: 610-619

Peltier, T.C., and P.S. Barboza. 2003. Growth in an Arctic grazer: effects of sex and dietary nitrogen on yearling muskoxen. Journal of Mammalogy 84: 915–925.

Barboza P.S. and R. T. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. Alces 37: 275-292.

Barboza, P.S., and R.T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. Journal of Mammalogy 81:473-479.

Relevant literature for R. and Dr. J. Cook:

Cook, R.C., T.R. Stephenson, W.L. Meyers, J.G. Cook, and L.A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934-1943.

Johnson, B.K., M.J. Wisdom, and J.G. Cook. 2005. Issues of elk productivity for research and management. North American Wildlife and Natural Resources Conference 69:551-571.

Cook, R.C., J.G. Cook, and L.D. Mech. 2004. Nutritional condition of Northern Yellowstone elk. Journal of Mammalogy 85:714-722.

Cook, J.G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. Delcurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155. 61 pp.

Cook, R.C., J.G. Cook, and L.L. Irwin. 2003. Estimating elk body mass using chest-girth circumference. Wildlife Society Bulletin 31:536-543.

Cook, R.C., J.G. Cook, R.A. Garrott, L.L. Irwin, and S.L. Monfort. 2002. Effects of diet and body condition on fecal progestagen excretion in elk. Journal of Wildlife Diseases 38:558-565

Cook, J.G. 2002. Nutrition and food habits. Pages 259-349 in D.E. Toweill and J. W. Thomas, editors, North American elk: ecology and management, Smithsonian Institution Press, Washington, D.C., USA.

Cook, R.C., D.L. Murry, J.G. Cook, P. Zager, and M.J. Gratson. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79:845-853.

Cook, R.C., J.G. Cook, D.L. Murray, P. Zagar, B.K. Johnson, and M.W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973-987.

Cook, R.C., J.G. Cook, D.L. Murray, P. Zagar, B.K. Johnson, and M.W. Gratson. 2001. Nutritional condition models for elk: which are the most sensitive, accurate, and precise? Journal of Wildlife Management 65:988-997.

Riggs, R.A., A.R. Tiedemann, J.G. Cook, T.M. Ballard, P.J. Edgerton, M.Vavra, W.C. Krueger, F.C. Hall, L.D. Bryant, L.L. Irwin, and T. Delcurto. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains Ecological Province. U.S. Forest Service, Pacific Northwest Research Station, Research Paper PNW-RP-527. 77pp.

Cook, J.G., L.L. Irwin, L.D. Bryant, R.A. Riggs, and J.W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildlife Monographs 141. 61p.

Garrott, R.A., J.G. Cook, J.G. Berardinelli, P.J. White, S. Cherry, and D.B. Vagnoni. 1997. Evaluation of the urinary allantoin:creatinine ratio as a nutritional index for elk. Canadian Journal of Zoology 75:1519-1525.

Cook, J.G., L.J. Quinlan, L.L. Irwin, L.D. Bryant, R.A. Riggs, and J.W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. Journal of Wildlife Management 60:528-541.

Cook, J.G., R.J. Hershey, and L.L. Irwin. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. Journal of Range Management 47:296-302.

Cook, J.G., and L.L. Irwin. 1992. Climate-vegetation relationships between the Great Plains and Great Basin. American Midland Naturalist 127:316-326.

Relevant literature for Dr. Sleep:

Brown, G., L. Landriault, D.J.H. Sleep, F. Mallory. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Submitted for publication.* Oecologia.