

MODELING THE IMPACT OF MOOSE AND WOLF MANAGEMENT ON PERSISTENCE OF WOODLAND CARIBOU

Réhaume Courtois^{1,2} and Jean-Pierre Ouellet³

¹Ministère des ressources naturelles et de la faune, Direction du développement de la faune, 880, ch. Ste-Foy, 2e étage, Québec, PQ, Canada G1S 4X4; ²Université Laval, Département de foresterie et de géomatique, Cité Universitaire, Ste-Foy, PQ, Canada G1K 7P4; ³Jean-Pierre Ouellet, Université du Québec à Rimouski, Département de biologie, Centre d'études nordiques, 300, allée des Ursulines, Rimouski, PQ, Canada G5L 3A1

ABSTRACT: Limiting factors of caribou (*Rangifer tarandus*) populations vary regionally. In tundra environments, this species appears to be regulated by food, either because wolves (*Canis lupus*) are absent or because migration of caribou allows escape from predation during part of the year. In the boreal forest, the main limiting factors are hunting and predation but because of low caribou densities, no regulation mechanism seems to exist between caribou and wolves. Moose (*Alces alces*) is the primary prey species of wolves and consequently, if moose abundance increases, wolves should also increase, independently of the caribou population. Thus, caribou could experience high predation rates and be eliminated in high wolf densities. Here we attempted to identify the necessary conditions to maintain caribou numbers in the presence of moose. To do so, we built a deterministic model that simulated the relationship between a caribou population regulated by food competition and limited by predation, a moose population regulated by predation, and a wolf population, the abundance of which is determined by moose abundance. At current hunting rates for caribou and moose in the boreal forest, and in the absence of wolf trapping, the model predicted that the caribou population would be extirpated in approximately 100 years. Wolf trapping was not adequate to conserve the caribou population unless very intensive control was undertaken. In the absence of trapping, cessation of caribou hunting allowed a 3-fold increase in caribou numbers over the long term, if the moose population remained low. According to our model, the best management measure for caribou consisted of maintaining a low moose density through appropriate population and habitat management strategies, which prevented expansion of the wolf population and limited predation on caribou.

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The hypothesis of exploitation ecosystems predicts that the number of trophic levels and population regulating factors depend on the primary productivity of an ecosystem (Oksanen et al. 1981, Oksanen and Oksanen 2000). In very poor environments (e.g., high arctic and deserts, where productivity is < 40 g/m²/year), ecosystems consist of vegetation communities that are regulated by competition for resources. In poor environments (e.g., tundra: 40 – 700 g/m²/year), plants are regulated by herbivores. In contrast, more productive environments are made up of three trophic levels that are regulated from the top.

Here, herbivores are regulated by carnivores that have only a limited impact on vegetation (Oksanen 1988), so both carnivores and plants are regulated by intraspecific competition.

Because regulating factors of caribou (*Rangifer tarandus*) vary between ecotypes, the exploitation ecosystem model seems appropriate for prediction of caribou population changes. In tundra environments, low productivity and low carrying capacity contribute to the establishment of undiversified biological communities. Predators are even absent on certain Arctic islands (Klein 1968, Ouellet et al. 1996) and in such cases, caribou

populations are regulated by competition for food and population changes can be described by a logistic model (Caughley 1977). Net population growth rate varies with density: populations increase exponentially at first and then growth rate gradually slows down as populations approach carrying capacity. In such environments, the carrying capacity seems to be on the order of 60–100 caribou per 100 km², as observed on Coats Island in Hudson Bay where caribou have occurred since at least the beginning of the 20th century (Ouellet et al. 1996). Massive mortalities from starvation sometimes take place overwinter due to food overexploitation or density-independent factors, such as climatic conditions preventing access to food (e.g., ice crust; Klein 1968, Reimers 1982).

In continental tundra, caribou populations also seem to be regulated by food. Caribou may undertake very long migrations that allow escape from predation most of the year, partly because wolf (*Canis lupus*) packs are confined to an exclusive territory, but mostly because wolf packs cannot move away from a den site when raising pups during summer (Bergerud 1996). In tundra environments, predation can be a significant limiting factor, but predation rate does not increase as a function of caribou abundance. Caribou numbers can therefore increase and, at high density, they can overexploit food available during summer (Bergerud 1996, Crête and Doucet 1998) or winter (Ouellet et al. 1994, 1996, 1997). As resources available per animal diminish with increasing population, a decrease in birth rate and an increase in adult and calf mortality are noted. Densities averaging 60 – 110 caribou per 100 km² have been observed in this environment (Messier et al. 1988, Seip 1991). Using the annual increase in lichen biomass, which is the primary food source for caribou (Gauthier et al. 1989), along with losses caused by animal trampling, Arsenault et al. (1997) have estimated the carrying capacity of caribou in tundra at approximately

20 animals per 100 km².

In the boreal forest, the carrying capacity for caribou is not precisely known. Based on lichen biomass, Crête and Manseau (1996) estimated that carrying capacity should be at least that observed in tundra, because alternative food sources (such as leaves, twigs, and deciduous shrubs) are abundant and the climate is milder in that environment. For example, in east-central Québec, carrying capacity based solely on terrestrial lichen has recently been estimated at 4.1 – 7.7 caribou per 100 km² (Courtois 2003). Despite a relatively high potential carrying capacity, woodland caribou populations experience very low densities of between 1 and 3 individuals per 100 km² (Seip 1991, Courtois 2003) and most are declining in North America (Mallory and Hillis 1998). Those observations suggest that woodland caribou populations are not regulated by intraspecific competition for winter food. Moreover, as caribou food habits are much less restrictive in summer, the main limiting factors seem to be hunting and predation (Stuart-Smith et al. 1997, Rettie and Messier 1998).

Caribou densities in the boreal forest (1 – 3 per 100 km²; Seip 1991, Courtois et al. 2003) are typically incapable of supporting wolf populations. Wolves in the boreal forest therefore depend on moose (*Alces alces*), a larger and more abundant ungulate that generally lives at densities of between 10 and 20 individuals per 100 km² (Messier 1985). Due to the absence of a regulating mechanism between caribou and wolves in the boreal forest (Seip 1991), an increase in moose abundance should provoke a wolf population increase, independent of caribou abundance. In such a situation, more frequent encounters between wolf and caribou should be expected leading to an increased predation rate on caribou that could decline, eventually down to extirpation (Seip 1991). Caribou abundance decreases when there are more than 0.60 – 0.65 wolves per 100 km² (Bergerud and Elliot 1986, Berg-

erud 1996) and caribou populations increase when wolf numbers are controlled (Boertje et al. 1996, Hayes et al. 2003).

The necessity for caribou to adopt avoidance strategies of both predators and other ungulates in order to survive is now recognized by the scientific community (Bergerud et al. 1984; Bergerud 1985, 1996; Seip 1991, 1992; Cumming et al. 1996; Stuart-Smith et al. 1997; Rettie and Messier 1998). However, the mechanisms underlying caribou, moose, and wolf interactions still remain obscure.

In this study, we built a deterministic model that mimicked the relationships between moose, wolves, and caribou and then simulated how variation in hunting of caribou and moose and in wolf trapping could influence caribou abundance. Model results should help to determine which management strategies are most suitable to maintain equilibrium between these three species in order to help maintain caribou, a threatened species in the boreal forest.

METHODS

The Model

The model simulates changes in caribou, moose, and wolf numbers in a 1,000-km² study area of the Québec boreal forest where the three species live in sympatry. According to the model, in the absence of wolves, the moose and caribou populations are regulated by food competition and follow a logistic equation ($N_{t+1} = N_t \times r \times [1 - N_t/KCC]$, where N_t and N_{t+1} = numbers at time t and time $t+1$, respectively, r = maximum population growth rate, and KCC = food carrying capacity; Caughley 1977). In the presence of wolves, the moose population is regulated by predation in accordance with the predation model of Messier (1994). Wolf numbers are determined by moose numbers, as predicted by the Michaelis-Menten hyperbolic equation of Messier (1994). In the combined model, where the three species interact, wolves have access to caribou and carry out density-independent

predation on that species, thus influencing survival of calves and adults, as predicted by the Bergerud and Elliot (1986) model. We completed the model by adding management parameters, which allowed changing the moose and caribou hunting and wolf trapping mortalities that were additive to natural mortality. Additional parameters allowed stochastic variation of moose and caribou productivity due to uncontrolled environmental conditions (Crête and Courtois 1997). The model (Appendix I) was elaborated using Stella 4.0 software (ISEE Systems, Lebanon, NH, USA).

In summary, our combined model is based on five postulates: (1) in the absence of predation or when predators are controlled, caribou and moose populations are regulated by competition for food (Messier 1994, Crête and Manseau 1996); (2) in the presence of wolves, the moose population is regulated by wolf predation (Messier 1994); (3) wolf numbers are determined by moose abundance (Messier 1994), but there is no dependence of wolves on caribou numbers (Seip 1991); (4) caribou predation increases non-linearly with wolf abundance (Bergerud and Elliot 1986); and (5) there is no immigration or emigration in the system or these two opposite processes are equal.

Caribou Population Parameters

Due to the paucity of woodland caribou population dynamics data, maximum growth rate and food carrying capacity were taken from published data for barren-ground caribou. Maximum population growth rate of caribou was based on observations of a population reintroduced on Southampton Island in Hudson Bay (Ouellet et al. 1996, 1997). In 1991, this population was estimated at $13,700 \pm 1,580$ adults, with an annual growth rate (r) of 0.245 since the introduction of 38 one-year-old individuals in 1967 ($N_t = N_0 \times e^{rt}$, hence $13,700 = 38 \times e^{r \times 24}$; where N_t = number of caribou at time t , N_0 = number of caribou in 1967, and t = time in years). No decline in growth

rate was observed over the 24 years, so this value of r should be close to the maximum attainable by a caribou population that is subject to negligible hunting ($< 1\%$ per year) and lacks wolf predation. Maximum growth rate is comparable to that reported for the caribou herd introduced on St. Matthew Island in the Bering Sea (17 – 29%; Klein 1968).

Carrying capacity based on availability of terrestrial lichens was estimated at 20 caribou per 100 km² (Crête and Manseau 1996, Arsenault et al. 1997). Caribou can eat various items (arboreal lichens, deciduous leaves, sedges, forbs, etc.), but these were not included in the carrying capacity estimates to avoid overestimation since winter diet is largely dominated by terrestrial lichens (Gauthier et al. 1989) and this season is the most likely to be limiting caribou (Klein 1968). Initial winter density was set at 1.63 individuals per 100 km², with 16% calves in the population, as noted in a recent aerial survey (Courtois et al. 2003). Annual losses due to predation and hunting (adults only) were initially established at 3% and 8%, respectively, as noted in central Québec (Courtois 2003). We considered that using empirical data would allow more realistic simulations for the Québec boreal forest.

Moose Population Parameters

Maximum annual growth rate of the moose population was estimated to be 25%, based on observations in Newfoundland in the absence of predation (Fryxell et al. 1988). Similar rates of increase were reported in south-central Québec (23-24%, Laurian et al. 2000). Other parameters were taken from studies carried out in east-central Québec where densities are approximately 3.0 moose per 100 km² (Gingras et al. 1989). The habitat carrying capacity was estimated at 84 moose per 100 km², based on annual production of deciduous twigs available during winter (Courtois et al. 1993). Although this estimate may appear low, it is four times higher than the minimum density required to maintain viable wolf populations (20 moose

per 100 km²; Messier 1985). Natural mortality rate was set at 9.2% per year (of which 4.5% was due to causes other than predation) while annual hunting mortality was estimated to be 9.0% (Courtois et al. 1994b). As for caribou, these estimates were the only ones available for the Québec boreal forest. Additional simulations involved annual stochastic variation in birth rate in order to mimic productivity changes (0.56 – 1.00) that were caused by variations in snowfall and summer temperature (Crête et Courtois 1997). It would have been possible to use stochastic variability in all parameters but we preferred using actual estimates to allow realistic simulations for the study site. Besides, anthropogenic mortality does not vary substantially from year to year because hunting regulation remains stable in the area. Finally, interpretation would have been difficult with simultaneous changes in many parameters.

Wolf Population Estimation

Our model considers wolf population size to be determined by moose population size, according to the predation model developed by Messier (1994, 1995) from 27 North American studies. This author demonstrated that it was possible to predict wolf abundance as a function of moose density (numerical response: number of wolves/1,000 km² = 58.73 × [number of moose/km² – 0.031]/[0.76 + number of moose/km²], $r^2 = 0.62$). The number of moose killed during winter (killing rate) first increases exponentially as a function of prey density then decelerates and starts declining at 0.65 moose/km² (functional response: number of moose killed per wolf per 100 days = 3.3 × number of moose per km²/[0.46 + number of moose per km²], $r^2 = 0.53$; Messier 1994). In this model, the total response is the product of numerical and functional responses. Following recommendations of Messier (1994), a correction factor of 0.71 was applied to winter predation rates to obtain annual rates and values for 100 days were converted to

annual values.

The impact of wolves on the caribou population was estimated using the Bergerud and Elliot (1986) density-independent model that was based on 17 North American studies. We thus predicted annual recruitment rate (percentage calves during winter = $e^{(3.340-0.127 \text{ wolves}/1,000 \text{ km}^2)}$, $r^2 = 0.69$) and annual mortality rate of adults (percentage adult mortality = $4,766 + (0.699 \text{ wolves per } 1,000 \text{ km}^2)^{1.275}$, $r^2 = 0.73$).

Simulations

Parameters and initial and calculated variables are presented in Appendix II. Preliminary simulations were performed on caribou and moose populations separately using the logistic model. These first analyses illustrated the trajectories of populations that were simply regulated by intraspecific competition for food. In a second trial, we used the moose-wolf model of Messier (1994) to illustrate the reaction of wolves in the presence of moose only. After these preliminary trials, we ran the combined model using the three species' interactions to investigate the outcome of a limited number of realistic management scenarios over a 100-year span. Four deterministic scenarios were conducted. In the first scenario, we simulated (1) population trajectories under management strategies that had prevailed in central Québec until autumn 2000 (i.e., moose and caribou hunting at 9% and 8%, respectively, but no wolf trapping). Then we successively simulated effects of (2) a caribou hunting ban; (3) intensive wolf trapping (at 30%; Larivière et al. 2000), and (4) moose hunting increased to 15% (in order to allow only a light population increase) without wolf trapping. Finally (5), in order to experiment with the effects of changes not controlled by harvest regulation, we included negative effects of stochastic environmental variations on productivity (Crête and Courtois 1997) of moose (from 0%–40%) and caribou (20%), on scenarios 1 and 2.

RESULTS

Simple Models for Caribou, Moose, and Wolf Populations

In the absence of hunting and predation, caribou reached their carrying capacity (K) in 53 years, with numbers increasing from 16 to 200 individuals in the 1,000-km² site. Half of the carrying capacity (optimal density $\approx 0.5K$) was reached in 10 years, allowing a maximum sustainable yield of 12 caribou per year in a stable population of 100 individuals. Adding a natural mortality of 3% resulted in 0.5 K being reached in 12 years, with a maximum sustainable yield of 9 individuals per year. When an additional anthropogenic harvest of 8% was included, the population reached 0.5 K after 28 years and did not exceed 112 caribou after 100 years.

In the absence of hunting and predation, the 30 initial moose reached their carrying capacity (840 individuals) in 62 years. The maximum sustainable yield (52 moose) was attained with a population of 420 moose (optimal density: 42 moose per 100 km²) in 13 years. Including a natural mortality of 9% resulted in 0.5 K being reached in 25 years, but the total population did not exceed 537 moose after 100 years. After adding another 9% hunting mortality, the population comprised only 234 moose (0.28 K) after 100 years.

According to the predation model (Messier 1994), the wolf population was sustained by the moose population and also regulated moose numbers. Both wolf abundance and predation rate increased with moose abundance. Without hunting, the moose population stabilized at 650 individuals (65 moose per 100 km²). At this plateau, predator density reached 2.58 wolves per 100 km², as predicted by the numerical response equation of Messier (1994).

Combined Model Incorporating Interactions Between Moose, Wolves and Caribou

Scenario 1: moderate moose (9%) and caribou (8%) hunting but no wolf trapping.— When moose and caribou were exploited at moderate rates and in the absence of wolf trapping, moose abundance increased from 30 to 110 individuals in 55 years and then remained stable (Fig. 1). Simultaneously, wolves increased from 0 at the start of the run to 5 individuals after 30 years only to stabilize afterwards. Moose predation rate reached 8% per year, which stabilized the moose-wolf system. Caribou abundance increased from 16 to 40 individuals in 14 years and then gradually declined to quasi-extirpation in 100 years (2 caribou remaining). The caribou decline initiated when moose and wolf reached 76 and 32 individuals (7.6 and 0.32 individuals per 100 km²), respectively.

Scenario 2: ban on caribou hunting with 9% moose hunting and no wolf trapping.— Cessation of caribou hunting did not influence the moose and wolf population trajectories, since the relevant population parameters remained the same (Fig. 2). The caribou hunting ban allowed the caribou population to increase and reach 94 individuals after 22 years; however, despite this increase, the caribou population started to decline as soon as moose numbers attained 95, thus supporting 4.5 wolves (9.5 moose and 0.45 wolves per 100 km²). Caribou were not extirpated and the population stabilized at approximately 64 individuals (6.4 per 100 km²).

Scenario 3: intensive wolf trapping (30%) with 9% moose and no caribou hunting.— Introducing intensive trapping of wolves (30%) to parameters of the previous simulation did not markedly improve the situation for caribou. Wolf abundance increased steadily despite exploitation, in parallel with the increase in moose abundance (Fig. 3). Abundance after 100 years was 5 wolves and 141 moose (0.5 and 14.7 per 100

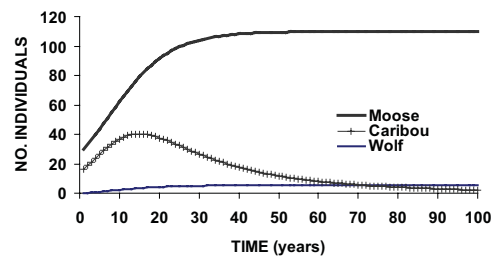


Fig. 1. Moose, wolf, and caribou population trajectories with moderate moose (9% per year) and caribou (8% per year) hunting but no wolf trapping (Scenario 1).

km², respectively). The caribou population reached 109 individuals after 23 years, but then declined and stabilized at (75 individuals 7.5 per 100 km²).

Scenario 4: increased moose hunting (15%) with no wolf and caribou harvesting.— Intensifying moose harvest to 15% but discontinuing wolf trapping maintained the moose population at a relatively low level of 61 individuals (6.1 moose per 100 km²), which directly reduced the wolf population to less than 2.2 individuals (< 0.22 wolves per 100 km²; Fig. 4). This management strategy was very favourable for caribou and the population reached 146 individuals after 30 years and then stabilized at 141 caribou (14.1 per 100 km²).

Scenario 5: stochastic environmental variations.— With random annual variation in birth rates, each simulation followed a new trajectory (Fig. 5). Stochastic variation in moose birth rate generated annual fluctua-

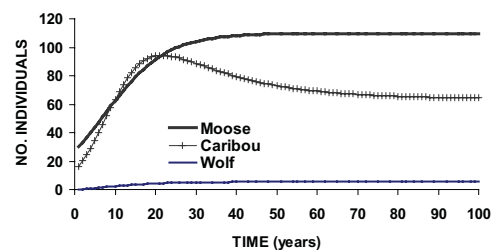


Fig. 2. Moose, wolf, and caribou population trajectories with moderate moose hunting (9% per year) but no caribou hunting or wolf trapping (Scenario 2).

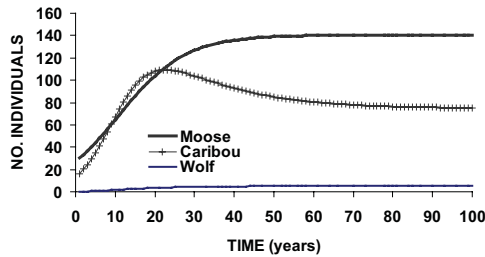


Fig. 3. Moose, wolf, and caribou population trajectories with moderate moose hunting (9% per year) and intensive wolf trapping (30% per year) but no caribou hunting (Scenario 3).

tions in both moose and wolf numbers, which always remained lower than in previous simulations. These variations had a positive impact on caribou numbers. In the presence of moderate moose harvesting (9%) but no wolf trapping or caribou hunting (previous scenario 2), the caribou population reached 125-135 individuals and stabilized at this level (Fig. 5a). If caribou hunting was also introduced into this model (previous scenario 1), the caribou population stabilized at approximately 50 – 60 individuals (Fig. 5b). When environmental stochasticity was allowed to increase the variation in caribou birth rate in addition to the moose birth rate, the caribou population declined to approximately 35 individuals (Fig. 5c).

Equilibrium Points of the Combined Models

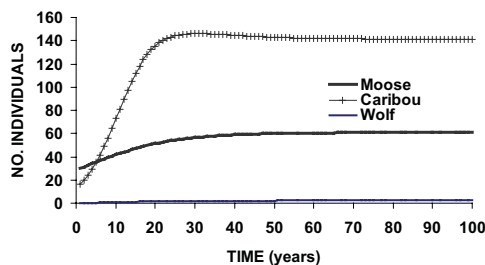


Fig. 4. Moose, wolf, and caribou population trajectories with moose hunting set at 15% per year but no caribou hunting or wolf trapping (Scenario 4).

Theoretical equilibrium points of the simple moose-wolf model were 65.0 moose and 2.58 wolves per 100 km². In the moose-wolf-caribou model, equilibrium points were much lower than these values. In simulations without stochastic environmental variation, equilibrium points were approximately 7 – 10

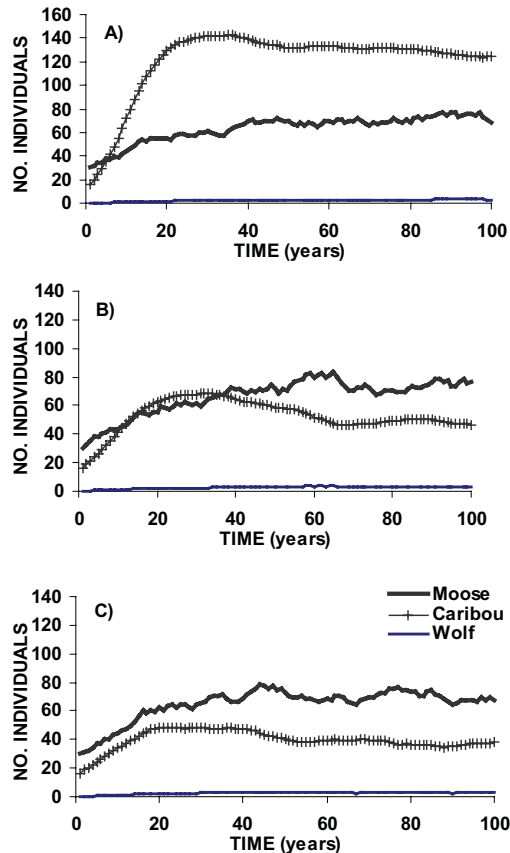


Fig. 5. Typical moose, wolf, and caribou population trajectories according to different management strategies and by including random variations in moose (all simulations) and caribou birth rates (last simulation) (Scenario 5). (A) Moderate moose hunting (9% per year), with no caribou hunting or wolf trapping; moose birth rate varying up to 40% a year; (B) Moderate moose (9% per year) and caribou (8% per year) hunting with no wolf trapping; moose birth rate varying randomly (0 – 40%); (C) Moderate moose (9% per year) and caribou (8% per year) hunting with no wolf trapping; both moose and caribou birth rates varying randomly, between 0 and 40% and 0 and 20%, respectively.

moose, 0.3–0.5 wolves, and 3–14 caribou per 100 km². In the last simulation, which appears a plausible situation in nature, populations stabilized at 6–8 moose, 0.2–0.3 wolves, and 3.5–4.0 caribou per 100 km².

DISCUSSION

Usefulness of the Combined Model in Caribou, Moose, and Wolf Management

Our moose-wolf-caribou model suggests interesting alternatives for the management of these three species. Seip (1991, 1992) proposed that predation could eliminate woodland caribou whenever wolves are sustained by another species because there is no retroactive mechanism that decreases the impact of wolves when the caribou population declines. Our simulations suggest that certain management strategies could help maintain caribou numbers by limiting wolf expansion. Wolf control could be considered (Bergerud and Elliot 1986, Seip 1991), but this strategy would only have a minor impact on caribou, unless a very intensive control is performed. Weclaw and Hudson (2004) obtained similar results using another model based on responses of wolves, moose, caribou, lichens, and vascular plants to various natural and anthropogenic factors. A 30% harvest rate exerted by trappers is not sufficient to limit wolf expansion. Due to a high birth rate, wolf populations can increase quickly if moose abundance is high.

Cessation of caribou hunting seems more efficient. This strategy should entail a tripling of the caribou population in the long term if the moose (and wolf) population does not increase significantly, which is the case when the habitat carrying capacity for moose is relatively low. Moose densities are generally higher in disturbed habitats and young forests rich in deciduous browse than in mature spruce forests (Timmermann and McNicol 1988). Moose expansion could therefore be controlled by limiting forest exploitation in sites used by caribou or by promoting spruce regeneration. Despite a strong influence of

wolves, our simulations suggest that caribou can be maintained in natural ecosystems, at least in the absence of human disturbance as suggested by Weclaw and Hudson (2004).

The best strategy, however, would consist of maintaining low moose densities through population and habitat management. Low moose densities imply low wolf densities and, therefore, low predation rates on caribou. Increasing the harvest of moose would be the easiest and most convenient management measure to adopt. Moose hunting is highly popular. With a 3- to 4-week hunting season, the harvest rate could reach 15% if all segments of the population (both sexes of adults and calves) were targeted without setting a limit on the number of hunting permits issued (Courtois et al. 1994a). In such a situation, our simulation suggests that moose density would stabilize at about 7–8 individuals per 100 km² and wolf density at less than 0.2–0.3 individuals per 100 km². Annual caribou recruitment would then be approximately 19–20% and adult predation rate would be around 7–8%. A population increase in caribou to 3–14 individuals per 100 km² could thus be seen in several decades. Even if conservative caribou hunting was maintained, a doubling or tripling of the population could be observed over the long term, depending on the magnitude of variations due to environmental factors. This scenario supports the growing evidence that moose management may be an integrated aspect of caribou management, as indicated by controlled experiments in the field (Hayes et al. 2003). We did not simulate moose hunting rates higher than 15% in order to maintain a stable or slightly increasing population. Management that encourages declining moose populations will lead to lower hunting success rate, which in the long term may be a less popular decision among hunters.

Our simulations seem optimistic in comparison with actual woodland caribou densities (1–3 individuals per 100 km², Seip 1991, Courtois 2003); however, historical densities

were much higher. Brassard (1967) measured a density of 26.2 caribou per 100 km² in a 25,723 km² study site in the boreal forest of the Québec North Shore. In Labrador, Bergerud (1967) estimated the 1958 density of the Mealy Mountain herd at 7.9 individuals per 100 km² over 30,303 km². Both these densities rapidly declined following intensive hunting during the 1960s and 1970s following the invention of snowmobiles that greatly facilitated hunter access. Similarly, caribou density was approximately 4 – 5 individuals per 100 km² in 1992 in the Charlevoix herd, north of Québec City, in the absence of hunting and restricted forest exploitation (Sebbane 2003). Caribou declines followed anthropogenic and natural habitat disturbance in the absence of hunting, presumably due to increased predation. Controlled experiments (Boertje et al. 1996, Hayes et al. 2003) and other simulation models (Weclaw and Hudson 2004) also suggest that caribou densities can attain 10 individuals per 100 km², depending on the extent of wolf predation and hunting-related mortality.

Effects of Increase in Caribou Biomass

We intentionally developed a simple model based on empirical data from the Québec boreal forest or the scientific literature in order to avoid including variables that were poorly quantified. In our model, wolf density depended exclusively on moose density. This hypothesis is justified because firstly, the presence of ungulates is necessary to sustain wolf populations (Messier 1994, 1995) and also caribou density was too low to constitute a sufficient food source. Another ungulate, the white-tailed deer, could be an important prey for wolves during winter, but this deer is not found where caribou live in the northern boreal forest. In sites used by woodland caribou, only the beaver is a significant food source for wolves. Although wolves certainly consume beavers in summer, which presumably increases pup survival, beavers are not readily available in winter because beaver movements

are mostly restricted to beneath the ice where food reserves are stored (Banfield 1974).

Nevertheless, we tested the effect of a possible caribou-wolf retroaction mechanism. We modified the 100-year model by assuming that the carrying capacity of wolves depended on the total biomass of available ungulates (Fuller 1989) and we considered that 1 caribou was equivalent to 0.29 moose, based on respective masses. As a result, the wolf population increased by 2% compared to scenario 2 (harvest rates: 9%, 0%, and 0% for moose, caribou, and wolves, respectively), which created population declines of 14% in moose and 6% in caribou. Assuming that wolves make hunting decisions based solely on prey biomass, not risk associated with their capture (which is lower for caribou than moose), the impact of an increase in wolves would probably be greater on moose than caribou.

Seip (1991) and Bergerud (1996) have suggested that caribou could be extirpated from an area in the presence of high moose densities due to increased predation on caribou from increased wolf densities. In contrast, Hayes et al. (2003) have suggested that reduced moose densities would lead to caribou extirpation in areas where wolves, moose, and caribou use similar habitats in summer because in such a case caribou lose the advantage of their spacing strategy to avoid predation. In the model including both moose and caribou biomass to support wolves, increasing the moose harvest rate to 22% led to extirpation of this species in 100 years, while caribou increased to 156 individuals. Despite a 10-fold increase, the caribou biomass (4.5 moose-equivalent per 100 km²) remained insufficient to support a viable wolf population that subsequently declined to 1 animal after 100 years, suggesting that an abundant primary prey (moose or deer) is required to maintain wolves in the boreal forest.

Our model implies that natural and anthropogenic mortality are additive. This assumption is probably valid for ungulates,

but wolf trapping could be partly compensatory (Fuller 1989). Harvesting wolves would indeed leave more food available for each surviving wolf, which could contribute to a wolf population increase. We did not have any empirical evidence to quantify this possibility, however. Moreover, if trapping is extensive, the reduced wolf packs should be less efficient in hunting, which would counter the benefits of an increase in available prey biomass per animal.

Limits of the Model

Simulation results are strongly dependent on which combinations of parameters are used and on the accuracy of the parameters included. Caribou and moose densities, food carrying capacity, and hunting mortalities were based on empirical data from the Québec boreal forest (Courtois 2003), but wolf densities and their related impact on caribou numbers could be greater than those predicted by our model. Larivière et al. (2000) used the number of wolf howls heard by hunters to predict wolf density. For the Port-Cartier – Sept-Îles Wildlife Reserve, which is located in the main distribution area of woodland caribou, these authors estimated a density of 0.85 wolves per 100 km². Using Fuller's model (1989), 0.48 wolves per 100 km² would be obtained. The model we used (Messier 1994) predicted 0.22 wolves per 100 km² for a similar moose abundance (6 individuals per 100 km²), and maximum density of 0.38 wolves per 100 km² at carrying capacity (84 moose per 100 km²). Only an inventory could provide accurate wolf numbers in the study area. However, if the wolf densities predicted by Larivière et al. (2000) and Fuller (1989) are correct, more restrictive measures would be needed to conserve caribou in the presence of moose and wolves. Similarly, the population growth rate for both caribou and moose is negatively influenced by certain environmental variables, such as snow conditions (Schaefer and Messier 1991). Therefore, simulations that do not include the

impact of such stochastic limiting factors are likely to yield optimistic results.

Bergerud and Elliot (1986) estimated that caribou abundance should decline when wolf density exceeds 0.65 individuals per 100 km². In our simulations, caribou numbers started declining as soon as the wolf population exceeded 0.45 individuals per 100 km². Caribou declines always followed an expansion phase, which means that food density-dependent mechanisms intervened when caribou numbers increased and that these mechanisms were additive to predation effects. The carrying capacity that we selected (20 caribou per 100 km², Arsenault et al. 1997) could also be too high based on recent estimates (4.1 – 7.7 individuals per 100 km², Courtois 2003), and recent studies suggest that caribou avoid human-related infrastructures leading to loss of available habitat (see Weclaw and Hudson 2004 for a review). Black bear (*Ursus americanus*) are not abundant in prime caribou habitat, but this species can exert an important additional density-independent pressure on caribou in some areas (Ballard 1994), particularly the southern region of the boreal forest. Therefore, the model may be inappropriate in areas with significant predation by black bear, grizzly bears, cougars, or other predators. Taken together, these findings advocate prudence in management decisions.

Model Improvements

Improvements could be made to our model. For example, the wolf population could be considered as a reservoir, rather than as a parameter linked to the moose population. This change would allow consideration of other variables that affect wolves, such as the presence of other prey species or demographic parameters specific to the study area. These uncontrolled variables and measurement errors were responsible for approximately 40% of the variance in wolf density between studies consulted by Messier (1994). The regulation mechanism between moose and wolves in our

model, however, seems more appropriate to mimic natural predator-prey dynamics than a priori parameters.

Furthermore, instead of considering ungulate populations as homogeneous reservoirs, we could categorize populations by age and sex classes to refine demographic outcomes. Such modifications would likely affect results only if proportions of males and females vary substantially. According to sensitivity analyses performed by Fancy et al. (1994), moose and caribou population growth rates are not highly sensitive to age structure, but rather depend on recruitment rate, which is strongly influenced by the proportion of adult females and their survival.

More importantly, a spatially explicit model would be particularly useful to investigate the possibility of excluding wolves from areas used by caribou, for example through habitat management that renders areas unsuitable for moose. Such a model could be based on the movement rate and direction of wolves between two feeding bouts. This refinement could help to determine the minimal size of a protected area for caribou that would permit avoidance of most encounters between wolves and caribou.

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REFERENCES

- ARSENAULT, D., N. VILLENEUVE, C. BOISMENU, Y. LEBLANC, and J. DESHAYE. 1997.

Estimating lichen biomass and caribou grazing on the winter grounds of northern Québec: an application of fire history and Landsat data. *Journal of Applied Ecology* 34:65-78.

BALLARD, W. B. 1994. Effects of black bear predation on caribou – A review. *Alces* 30:25-35.

BANFIELD, A. W. F. 1974. *Les Mammifères du Canada*. Les Presses de l'Université Laval, Québec, Québec, Canada.

BERGERUD, A. T. 1967. Management of Labrador caribou. *Journal of Wildlife Management* 31:621-635.

_____. 1985. Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology* 63:1324-1329.

_____. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer*, Special Issue 9:95-116.

_____, and J. P. ELLIOT. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515-1529.

_____, R. D. JAMINCHUK, and D. R. CARRUTHERS. 1984. The buffalo of the North: woodland caribou at calving. *Animal Behavior* 39:360-368.

BOERTJE, R. D., P. VALKENBURG, and M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management* 60:474-489.

BRASSARD, J. M. 1967. *Inventaire aérien des ongulés sauvages de la Côte-Nord et identification des aires d'hivernement en fonction des formes du relief et de la végétation*. Service de la Faune. Québec, Québec, Canada.

CAUGHLEY, G. 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, London, U.K.

COURTOIS, R. 2003. La conservation du caribou forestier dans un contexte de perte d'habitat et de fragmentation du milieu.

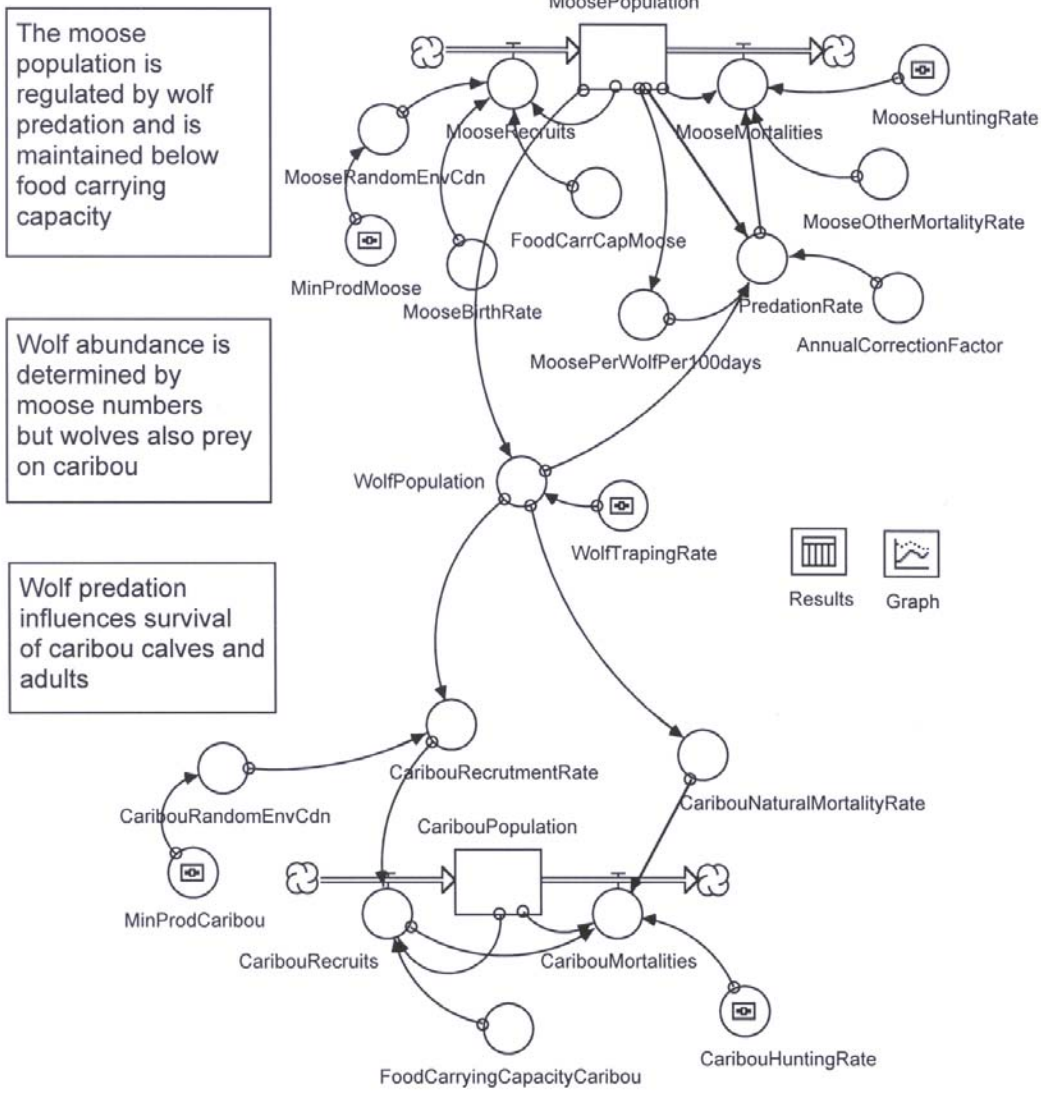
- Ph.D. Thesis. Université du Québec à Rimouski, Rimouski, Québec, Canada.
- _____, M. CRÊTE, and F. BARNARD. 1993. Productivité et dynamique d'une population d'originaux du sud de la taïga québécoise. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec, Canada.
- _____, A. GINGRAS, C. DUSSAULT, L. BRETON, and J.-P. OUELLET. 2003. An aerial survey technique for the forest-dwelling ecotype of woodland caribou, *Rangifer tarandus caribou*. *Canadian Field-Naturalist* 117:546-554.
- _____, Y. LEBLANC, J. MALTAIS, and H. CRÉPEAU. 1994a. Québec moose aerial surveys: methods to estimate population characteristics and improved sampling strategies. *Alces* 30:159-171.
- _____, D. SIGOUIN, J. -P. OUELLET, A. BEAUMONT, and M. CRÊTE. 1994b. Mortalité naturelle et d'origine anthropique de l'original au Québec. Ministère de l'Environnement et de la Faune. Québec, Québec, Canada.
- CRÊTE, M., and R. COURTOIS. 1997. Limiting factors might obscure population regulation of moose (*Cervidae: Alces alces*) in unproductive forests. *Journal of Zoology* 242:765-781.
- _____, and J. DOUCET. 1998. Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. *Arctic and Alpine Research* 30:126-132.
- _____, and M. MANSEAU. 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. *Evolutionary Ecology* 10:51-62.
- CUMMING, H. G., D. B. BEANGE, and G. LAVOIE. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. *Rangifer*, Special Issue 9:81-94.
- FANCY, S. G., K. R. WHITTEN, and D. E. RUSSELL. 1994. Demography of the Porcupine caribou herd, 1983-1992. *Canadian Journal of Zoology*. 72:840-846.
- FRYXELL, J. M., W. E. MERCER, and R. B. GELLATEL. 1988. Population dynamics of Newfoundland moose using cohort analysis. *Journal of Wildlife Management* 52:14-21.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.
- GAUTHIER, L., R. NAULT, and M. CRÊTE. 1989. Variations saisonnières du régime alimentaire des caribous du troupeau de la rivière George, Québec nordique. *Naturaliste Canadien* 116:101-112.
- GINGRAS, A., R. AUDY, and R. COURTOIS. 1989. Inventaire aérien de l'original dans la zone de chasse 19 à l'hiver 1987-88. Ministère du Loisir, de la Chasse et de la Pêche. Sept-Îles, Québec, Canada.
- HAYES, R. D., R. FARNEL, R. M. P. WARD, J. CAREY, M. DEHN, G. W. KUZYK, A. M. BAER, C. L. GARDNER, and M. O'DONOGHUE. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152.
- KLEIN, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* 32:350-367.
- LARIVIÈRE, S., H. JOLICOEUR, and M. CRÊTE. 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Québec. *Biological Conservation* 94:143-151.
- LAURIAN, C., J. -P. OUELLET, R. COURTOIS, L. BRETON, and S. St-ONGE. 2000. The effects of intensive harvesting on moose reproduction. *Journal of Applied Ecology* 37:515-531.
- MALLORY, F. F., and T. L. HILLIS. 1998. Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints/releases, and population dynamics. *Rangifer*, Special Issue 10:49-60.
- MESSIER, F. 1985. Social organization, spa-

- tial distribution and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63:1068-1077.
- _____. 1994. Ungulate population models with predation: a case study with North American moose. *Ecology* 75:478-488.
- _____. 1995. Trophic interactions in two Northern wolf-ungulate systems. *Wildlife Research* 22:131-146.
- _____, J. HUOT, D. LE HENAFF, and S. LUTTICH. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41:279-287.
- OKSANEN, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? *The American Naturalist* 131:424-444.
- _____, and T. OKSANEN. 2000. The logic and realism of the hypothesis of exploitation ecosystem. *The American Naturalist* 155:703-723.
- _____, D. STEPHEN, J. A. FRETWELL, and N. PEKKA. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118:240-261.
- OUELLET, J.-P., S. BOUTIN, and D. C. HEARD. 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. *Canadian Journal of Zoology* 72:1426-1435.
- _____, D. C. HEARD, S. BOUTIN, and R. MULDER. 1997. A comparison of body condition and reproduction of caribou on two predator-free Arctic islands. *Canadian Journal of Zoology* 75:11-17.
- _____, _____, and R. MULDER. 1996. Population ecology of caribou populations without predators: Southampton and Coats Island herds. *Rangifer*, Special Issue 9:17-26.
- REIMERS, E. 1982. Winter mortality and population trends of reindeer on Svalbard, Norway. *Arctic and Alpine Research* 14:295-300.
- RETTIE, W. J., and F. MESSIER. 1991. The implications of environmental variability on caribou demography: theoretical consideration. *Rangifer*, Special Issue 7:53-59.
- _____, and _____. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. *Canadian Journal of Zoology* 76:251-259.
- SEBBANE, A., R. COURTOIS, S. ST-ONGE, L. BRETON, and P. -É. LAFLEUR. 2003. Trente ans après sa réintroduction, quel est l'avenir du caribou de Charlevoix? *Naturaliste Canadien* 127:55-62.
- SEIP, D. R. 1991. Predation and caribou populations. *Rangifer*, Special Issue 7:46-52.
- _____. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494-1503.
- STUART-SMITH, A. K., J. A. COREY, S. BOUTIN, D. H. HEBERT, and A. B. RIPPIN. 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *Journal of Wildlife Management* 61:622-633.
- TIMMERMANN, H. R., and J. G. MCNICOL. 1988. Moose habitat needs. *The Forestry Chronicle* 64:238-245.
- WECLAW, P., and R. J. HUDSON. 2004. Simulation of conservation and management of woodland caribou. *Ecological Modeling* 177:75-94.

Appendix I

Stella model incorporating moose, wolf, and caribou interactions in the boreal forest. Rectangles represent reservoirs (populations), double arrows identify sources (births) and sinks (deaths), and circles represent parameters (variables) influencing sources and sinks. Simulations tested the impact of changes in caribou and moose hunting rates (CaribouHuntingRate and MooseHuntingRate, respectively), wolf trapping rate (WolfTrappingRate) and changes in caribou and moose productivity due to random variations in environmental conditions (CaribouRandomEnvCdn and MooseRandomEnvCdn) on caribou and moose reproductive rates. Other parameters and equations were obtained from the literature (see methods). MinProdCaribou and MinProdMoose indicate the minimum productivity of the species under the worst environmental conditions. Other acronyms are self explanatory.

Moose, wolf and caribou populations inhabiting a 1000-km² area



Appendix II

Parameters and variables used in the models, values employed in the simulations, and data sources.

Parameter or variable	Values employed	Data source
MOOSE		
Habitat carrying capacity	840 in the study area (84 per 100 km ²)	Courtois et al. (1993)
Population	30 in the study area at time 0; calculated by the model afterwards	Gingras et al. (1989)
Maximum growth rate	25% per year	Fryxell et al. (1988)
Annual predation rate	Calculated from Messier's predation model (depends on moose density)	Messier (1994)
Annual hunting rate	9% (simulations 1, 2, 3, 5) or 15% (simulation 4)	Courtois et al. (1994b)
Annual rate of mortality due to other causes	4.50%	Courtois et al. (1994b)
Annual variability of recruitment	0% (simulations 1 to 4); random variation between 0 and 40% (simulation 5)	Crête and Courtois (1997)
WOLF		
Population	Calculated from Messier's Michaelis-Menten hyperbolic equation (depends on moose population)	Messier (1994)
Trapping rate	0% (simulations 1, 2, 4, 5) or 30% (simulation 3)	Larivière et al. (2000)
CARIBOU		
Habitat carrying capacity	200 in the study area (20 per 100 km ²)	Arsenault et al. (1997)
Population	163 in the study area at time 0; calculated by the model afterwards	Courtois et al. (2003)
Maximum growth rate	24.5% per year	Estimated from Ouellet et al. (1996, 1997) data
Annual recruitment rate	Calculated from Bergerud and Elliot's model (depends on wolf density)	Bergerud and Elliot (1986)
Annual rate of adult natural mortality	Calculated from Bergerud and Elliot's model (depends on wolf density)	Bergerud and Elliot (1986)
Annual hunting rate	9% (simulations 1, 2, 3, 5) or 15% (simulation 4)	Courtois et al. (2003)
Annual variability of recruitment	0% (simulations 1 to 4, 5a and 5b); random variation between 0 and 20% (simulation 5c)	Arbitrary