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MANAGEMENT OF INDIGENOUS NORTH AMERICAN DEER AT THE END OF THE 20TH CENTURY IN RELATION TO LARGE PREDATORS AND PRIMARY PRODUCTION*

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Five deer species occupy North America: caribou (3.6×10^6 individuals), moose (1.1×10^6), white-tailed deer (28.5×10^6), mule deer (5.0×10^6) and wapiti (1.1×10^6). Caribou characterise the north of the boreal forest and the tundra, whereas moose dominate in coniferous and mixed forests growing further south. White-tailed deer are typical of the deciduous forests of the east while mule deer replace them in the mountainous terrain of the west. Wapiti possess the smallest range, mostly adjacent to the prairies to the west. The two large obligate carnivores preying on deer show a reduced distribution: wolves are almost restricted to Canada, and cougar to the mule deer range. We determined the current status of each species with the help of a questionnaire mailed to all jurisdictions harbouring deer. Most reports of threatened populations concerned caribou whereas many jurisdictions declared overabundance of white-tailed deer and wapiti. Hunting was allowed for all species when they abounded in a jurisdiction. Hunters harvested annually 7.0×10^6 deer on the continent, 87% being white-tailed deer. The two species that caused most conflicts with humans had the highest harvest rate: 16–17%. In terms of biomass, white-tailed deer and wapiti yielded the highest harvests, with 55 and 39 $\text{kg} \times \text{km}^{-2}$ of range, respectively. The average standing biomass of deer in winter ranged between 28 $\text{kg} \times \text{km}^{-2}$ in Nevada to 901 $\text{kg} \times \text{km}^{-2}$ in Indiana. The lowest standing biomasses occurred in the boreal forest (predators), in the prairies (agriculture) and in the south-west (aridity), and the highest ones in the south-east, where only white-tailed deer is present. The current abundance of deer in North America parallels, in general, the primary production of the landscape ($r^2 = 0.38$; $P < 0.0001$), but predators and human activity modify this pattern.

Key words: Caribou, elk, management, moose, mule deer, North America, white-tailed deer

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The common ancestor of the five extant North American deer appeared in Eurasia during the Miocene, and each species had differentiated by the Pliocene or early Pleistocene (Baker, 1984; Cronin, 1991*a*). Based on fossil records, white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) became distinct species the most recently, about 0.7–1.9 × 10^6 years ago (Baker, 1984; Carr and Hughes, 1993). These two species sometimes hybridise where their distribution overlaps (Cronin, 1991*b*; Derr, 1991; Balinger et al., 1992; Hughes and Carr, 1993); human activity and predator extirpation likely favoured increasing density and some expansion of white-tailed deer range during the current century, which increased contacts between the two species (Baker, 1984).

The current distribution of North American deer (Fig. 1) suggests that each species has developed adaptations better suited for its individual biome. Lichens make up the key element of caribou (*Rangifer tarandus*) forage (e.g. Gauthier et al., 1989), and not surprisingly caribou abound in the transition zone between the forest and the tundra where they form large migratory herds feeding on terrestrial lichen mats (Crête et al., 1996). Moose (*Alces alces*) distribution coincides with that of coniferous and mixed forests where they exploit in particular dense stands of deciduous shrubs (Crête and Courtois, 1997), characteristic of early serial stages or riparian communities. White-tailed deer occupy a wide range but perform best in the deciduous forests of eastern North America where they feed, during the growing season, on forbs and leaves of deciduous shrubs or trees (Healy, 1971; McCaffery et al., 1974; Skinner and Telfer, 1974). Mule deer also exploit forbs and leaves of trees (Deschamp et al., 1979; Hanley, 1984; Austin and Urness, 1985), but they are adapted to the mountainous terrain of the west. Some sub-species occupy relatively dry areas (Baker, 1984), whereas others, designed as black-tailed deer, are adapted to the humid forests of the north-west. Mule and black-tailed deer interbreed when their range overlaps (Cronin, 1991*b*). Wapiti (*Cervus elaphus*) consume a mixed diet of graminoids and forbs (Baker and Hobbs, 1982; Rowland et al., 1983; Hanley, 1984) and appear best suited for open forests that characterise the transition zone between the prairies and the forests. Wapiti occupied eastern North America at the arrival of the first Europeans, and based on reports of the first French explorers, they occupied the meadows bordering rivers (Anonymous, 1972).

The colonisation of North America by European settlers deeply modified the equilibrium that existed between aborigines and large mammals. The negative impacts of land clearing, venison demand and skin trade of deer on population size remained mostly limited to the east of the Appalachian Mountains and the St. Lawrence valley until 1800, when rapid human colonisation of the centre and the west of the continent started (McCabe and McCabe, 1984). In the case of white-tailed deer for example, population size may have fallen from 30 million individuals by the year 1500, to less than 1 million at the beginning of the current century, when states and provinces began protecting wildlife (McCabe and McCabe, 1984). Current populations mostly originated from local survivors in spite of numerous transplantation programs (Ellsworth et al., 1994). Colonisation of the continent also negatively affected deer predators, whose ranges shrank. The red wolf (*Canis rufus*) may have completely disappeared or at best has been reduced to insignificant numbers (Nowak, 1992; Roy et al., 1994). The current distribution of the two large obligate carnivores that are still abundant is almost completely restricted to Canada in the case of the gray wolf (*C. lupus*) and to the mule deer range in the case of the cougar (*Felis concolor*) (Fig. 2). Black bears, which can prey on deer fawns (Ballard, 1992), still occupy most of Canada and mountainous areas of USA, whereas brown bears, which can prey on either young or adult deer (Ballard, 1992), still persist in the north-west of the continent. All deer and their predators have been managed with increasing refinement by agencies responsible for wildlife since the middle of the 20th century.

Although the concept of regulation in population dynamics has been recently criticised as too simplistic (Rhodes and Odum, 1996), the relative stability of large mammal populations over ecological time scale and numerous studies indicate that density-dependent processes operate to keep numbers within a range set by the carrying capacity. Moreover, there exists no alternative to the theory developed by Caughley (1976) for the management of large ungulates. This theory rests on the assumptions of density-dependence and carrying capacity; this approach produces plausible predictions under the assumption of regulation either by predators (Crête et al., 1981) or by forage (McCullough, 1979; Nielsen et al., 1997). The modern distribution of wolves in North America limits the study of regulation of deer populations in presence of natural predators to caribou and moose. Although controversial, demographic studies on moose suggest that predation regulates moose density much below the level set by forage (predation-regulation hypothesis: Sinclair and Arcese, 1995) when gray wolves coexist with black or brown bear (Messier and Crête, 1985; Crête, 1987; Gasaway et al., 1992; Crête and Manseau, 1996; Crête, 1998). Predation would also regulate forest-dwelling caribou (Seip, 1991, 1992) whereas regulation would depend on forage for migratory herds (Crête et al., 1996). One study on mule deer of Vancouver Island indicated that wolf predation severely limited deer numbers (Hatter and Janz, 1994).

Crête and Manseau (1996) studied trophic interactions of caribou and moose on the Québec-Labrador peninsula between the tundra in the north and the mixed forests in the south, and came to the conclusion that their data supported the Fretwell–Oksanen hypothesis (Fretwell, 1977; Oksanen et al., 1981): due to the low productivity of the tundra, caribou numbers would be regulated by forage in this biome, whereas predators would regulate deer at low density in more productive landscapes. We hypothesised that the same trophic interactions would operate on the rest of the continent, and we predicted that wolves, in conjunction with bear, would regulate deer numbers at low density within the range wolves have traditionally occupied, and that forage would regulate deer numbers south of the wolf range, even in presence of cougar. The objectives of this paper were to describe the management of indigenous North American deer at the end of the 20th century and to test our working hypothesis on population regulation, using data on deer abundance.

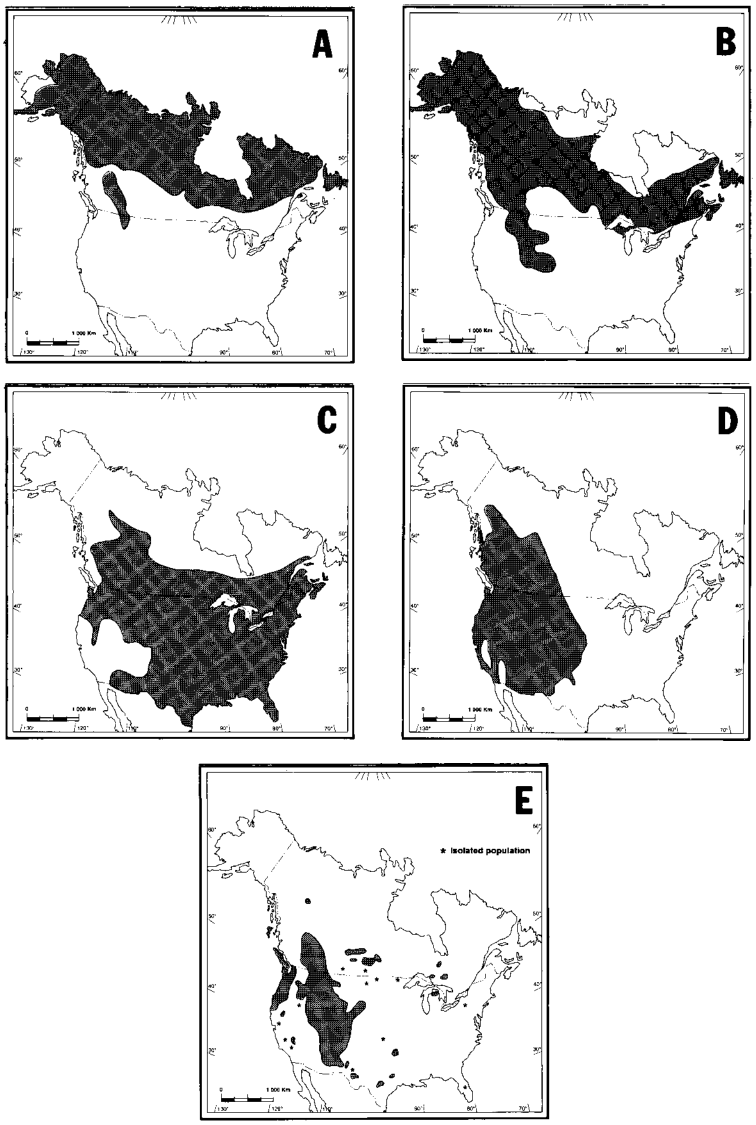

Fig. 1. Approximate distribution of North American deer at the end of the 20th century (A = caribou; B = moose; C = white-tailed deer; D = mule deer; E = wapiti) (after Schmidt and Gilbert, 1978; Thomas and Toweill, 1982; Halls, 1984; Anonymous, 1989)

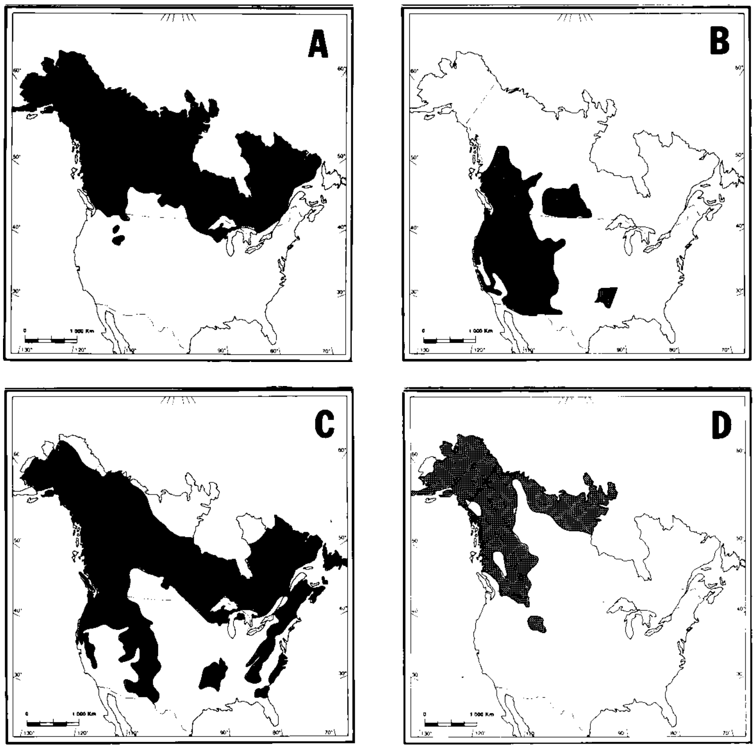

Fig. 2. Approximate distribution of North American large carnivores at the end of the 20th century (A = gray wolf; B = mountain lion; C = black bear; D = grizzly bear) susceptible to prey on deer (after Novak et al., 1987)

Methods

We used a questionnaire to collect the data necessary to achieve our goals. We mailed it to the 60 jurisdictions of North America responsible for deer management by mid-January 1998; we received the final answers in late April. We did not survey the District of Columbia (small and urban) and Prince Edward Island (no deer), and we considered separately the island of Newfoundland and Labrador, due to striking differences, although the same agency manages both areas. We tried to keep the questionnaire short in order to encourage deer managers to complete it and we tested it in two jurisdictions before the general mailing. We asked the population size and the area covered by the range of each species within each jurisdiction. We did not request specification of the techniques used for estimating population sizes, but all species can be surveyed from the air (e.g. Bartmann et al., 1986; Crête et al., 1986; Bear et al., 1989; Potvin et al., 1992; Couturier et al., 1996). We did not precise the period of the year for which we wanted estimations of population size, but most jurisdictions provided post-hunt estimates. In very few cases, respondents did not indicate population size or range area; we extrapolated these figures, based on harvest size they provided and comparisons with neighbouring jurisdictions. Other questions pertained to the presence of threatened or overabundant populations within the jurisdiction. We also requested managers to indicate the overall trend for each species: increasing, stable or decreasing. When data existed, we requested managers to indicate the number of deer killed in vehicle collisions; we extrapolated to the whole continent by cross multiplication with population size. Other questions pertained to hunting, when this activity was permitted. As we wanted to express yields and densities in terms of individuals and biomass, we asked respondents to provide figures on mean live mass of adult males, adult females and fawns. We requested information on licence issuance, on weapons used, on hunting season and on harvest size by sex/age categories for the period 1992–1996.

In order to determine how the biomass of deer was distributed on the continent, we added the standing winter biomass of each species within a jurisdiction and we divided this sum by the total area covered by the jurisdiction. As we did not know the composition of standing winter populations, we used the average body mass of females for converting deer numbers into biomass. We examined the relationship between average deer biomass per jurisdiction and average actual evapotranspiration (AE) in the centre of each jurisdiction using regression analysis (Proc REG, SAS Institute Inc., 1985); we transformed deer biomass into their natural logarithm in order to normalise the residues.

Results

At the end of the 20th century, there were almost 40 million deer in winter in North America (Table 1). White-tailed deer made 72% of them, while moose and wapiti were the least numerous, numbering each slightly more than 1 million individuals. Caribou, moose and white-tailed deer occupied equivalent and large ranges, covering 6–7 × 10^6 km^2, whereas wapiti had the most limited distribution, with 1.3 × 10^6 km^2. Very few jurisdictions reported the existence of threatened deer populations, most cases concerning forest dwelling or mountain caribou. By opposition, numerous managers reported problems of overabundance, in particular for white-tailed deer and to a lesser extent for wapiti. Moose, white-tailed deer and wapiti populations appeared particularly healthy as over half of the jurisdictions indicated increasing trends. On the other hand, mule deer and caribou had highest reports of decreasing size. We estimated that over 700,000 deer died annually in road accidents in North America, mostly white-tailed and mule deer.

Table 1

Status of indigenous North American deer by 1995–1996, as determined by a questionnaire completed by managers of the 60 jurisdictions harbouring deer

	Caribou	Moose	White-tailed deer	Mule deer	Wapiti
Population size (10^6)	3.64	1.05	28.55	5.07	1.07
Range (10^6 km^2)	7.03	6.44	6.30	3.78	1.30
Jurisdictions where present	13	28	55	23	30
Jurisdiction with populations (%)[a]					
threatened	46	7	4	4	10
overabundant	15	14	73	23	41
Population trend (%)[a]					
increasing	15	50	52	27	52
stable	54	38	35	27	38
decreasing	31	12	13	45	10
Annual number of road kills (10^3)[b]	< 1	5	618	81	9

[a]Percent jurisdictions where a given species is present; [b]Extrapolated from jurisdictions where the information was available

Most jurisdictions allowed hunting when a deer species was present, although caribou managers remained more prudent than others (Table 2). The annual deer harvest approached 7 million heads between 1992–1996 in North America, with white-tailed deer dominating (87% of the harvest). In terms of yield per surface area, white-tailed deer and wapiti produced annually 55 kg and 39 kg × km^{-2} of range, respectively, 20–25 times more than caribou. Not surprisingly, white-tailed deer and wapiti suffered the highest harvest rate, i.e. 17 and 16%, respectively. Adult males dominated in the harvest, but adult females made up ≈ 40% of the take for the two species most heavily exploited. Rifles represented the dominant weapon used for culling deer, except in jurisdictions with dense human populations, where shotguns replaced them. In general, managers achieved their harvest goals by limiting the number of licences issued, sometimes by sex/age categories; systems of licence issuance varied widely. Harvesting appeared more liberal with overabundant white-tailed deer or in some northern jurisdictions where Native people hunted year long. All hunting seasons began in late summer or autumn, with caribou hunt being the earliest and white-tailed deer the latest. Based on managers' reports, adult male moose weighed ≈ 450 kg, by comparison to ≈ 300 kg for wapiti. White-tailed deer and mule deer averaged very similar life body mass, i.e. 65–70 kg for adult males.

Table 2

Selected statistics pertaining to the hunting of North American deer between 1992–1996 and mean live body mass (± SE; n) as reported by managers. Besides harvest size and biomass harvested × km^{-2} which are exact counts, we computed means over all responding jurisdictions without weighting by harvest size

	Caribou	Moose	White-tailed deer	Mule deer	Wapiti
Jurisdictions allowing hunting (%)	62	86	98	91	86
Annual harvest size (10^3)	121	85	6040	535	196
Biomass harvested (kg×km^{-2})	2	5	55	9	39
Harvest rate (%)	3	8	17	9	16
Harvest composition (%)					
males	N.A.[a]	68	53	77	53
females	N.A.	21	37	21	43
fawns[b]	N.A.	11	10	2	4
Jurisdictions issuing unlimited number of licences (%)	22	10	33	23	12
Mean opening date of the hunting season	08–16	09–25	11–06	10–18	10–12
Live body mass (kg)					
males	159 (14; 5)	442 (43; 8)	66 (3; 35)	68 (2; 10)	305 (37; 9)
females	109 (9; 5)	330 (28; 7)	52 (2; 33)	54 (3; 10)	214 (15; 9)
fawns	48 (7; 5)	139 (12; 7)	32 (2; 31)	33 (3; 8)	84 (10; 6)

[a]not available; too many unclassified specimens; [b]biaised downward because fawns were grouped with females in some jurisdictions

When combining all species in terms of standing deer biomass, a general pattern emerged for North America. The lowest densities occurred in the boreal forest and the tundra, in the prairies and in south-western United States (Fig. 3). In comparison, the highest standing biomasses of deer were concentrated in the south-east quarter of the continent. Extremes varied between 28 kg × km^{-2} in Nevada and 901 kg × km^{-2} in Indiana. The standing deer biomass averaged 95 kg × km^{-2} in continental Northwest Territories and northern Québec (600,000 km^2), which corresponds to the distribution of the large Canadian migratory herds of caribou; we excluded Alaska in this computation because this state may be less homogenous than the rest of the continent with respect to the distribution of the tundra and the boreal forest; we also excluded Yukon because migratory caribou are seasonally resident only. In the range which moose shared with established gray wolf populations in the centre of the continent (British Columbia to southern Québec; Yukon excluded), the combined deer biomass averaged 62 kg × km^{-2}, which contrasts with 299 kg × km^{-2} in the rest of the moose range where wolves were very rare or absent [Maritimes Provinces (absent), northern New England (absent) and north-west USA (rare, recolonising)].

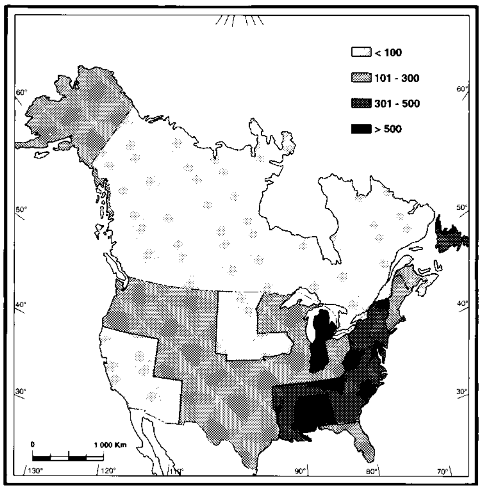

Fig. 3. Average winter standing biomass (kg × km^{-2}) of deer per jurisdiction when combining all indigenous North American species; data were grouped in 4 classes. Total biomasses were divided by the whole area covered by each jurisdiction without correcting for unsuitable habitat, i.e. human dwellings, agricultural lands, etc.

Discussion

Management of North American deer

With almost 40 million deer and no species counting less that 1 million individuals at the end of the 20th century, North American managers should be satisfied with the recovery of cervidae since their decline created by the European colonisation of the continent. Some populations or sub-species living in peripheral ranges may be threatened or endangered (Jabbour et al., 1997), but no deer species risks disparition in a foreseeable future in North America. The conservation of forest-dwelling caribou which live at low density (1–3 × 100 km^{-2}; Seip, 1991) in presence of increasing forest exploitation likely poses the greatest challenge to deer managers; many declining mule deer populations also cause concerns.

Most jurisdictions now possess the tools and the expertise for adequately conserving deer. Jurisdictions are divided into management units for which target densities and harvests are set when hunting is permitted. The issuance of licences and the length of the hunting seasons control the harvest size, whereas periodic surveys allow the measurement of population response. Citizens support deer managers by massively respecting hunting regulations. Our questionnaire included a request to estimate poaching, but many respondents hesitated to estimate it without hard data; those who did, indicated that illegal killing of deer affected only a small fraction of populations.

We estimated that the annual harvest rate averaged 17% and 16% for white-tailed deer and wapiti, respectively, and much lower for the other deer. These figures are far below the maximum finite rate of increase of North American deer which can vary between 80% ($\lambda = 1.80$) for white-tailed deer on good ranges (Crête and Lemieux, 1996) and 34% ($\lambda = 1.34$) for caribou colonising forage-rich areas (Heard, 1990). Maximum λ sets the extreme values that could reach harvest rates if hunting was the only mortality factor for deer. Using Caughley's (1976) approach, we are forced to conclude that, overall, the management of North American deer is currently conservative, and that most populations have been recently kept at density close to the carrying capacity of their range. As forage appears to regulate deer numbers at high density in many areas devoid of natural predators, overabundant deer create problems with humans, other animal species and the vegetation. In particular, white-tailed deer threaten many forest herbs (Miller et al., 1992), affect tree composition (Anderson and Katz, 1993) and slow down forest regeneration (Marquis, 1981). At the end of the 20th century, hunting remains the most economic tool for controlling deer numbers and for minimising social and conservation problems in North America. However, this activity belongs more to the rural than to urban culture, and it is uncertain whether hunters will remain numerous enough in the future to achieve target harvests, given increasing concentration of people in cities and social pressure against the killing of animals.

Deer number in North America vs. large predators and forage abundance

We made our prediction concerning deer abundance on the continent based on observations made on the Québec-Labrador peninsula (Crête and Manseau, 1996). In Québec, the standing deer biomass averaged 180 $\mathrm{kg} \times \mathrm{km}^{-2}$ in the range of migratory caribou, 15 $\mathrm{kg} \times \mathrm{km}^{-2}$ in unproductive boreal forests where caribou and moose coexisted, and 100 $\mathrm{kg} \times \mathrm{km}^{-2}$ in the core of the moose range. Considering forage and predator abundance, Crête and Manseau (1996) concluded that their data set fit the Fretwell–Oksanen hypothesis (Fretwell, 1977; Oksanen et al., 1981), which pertains to trophic interactions in ecosystems. In the less productive area (northernmost), the food chain would be limited to two functional trophic levels and forage availability would determine the abundance of herbivores. With increasing primary production (the two southernmost sites), the food chain would extend to three functional levels, and predators would keep herbivore density much below the carrying capacity set by forage. The observation that the standing biomass of moose climbed to 740 $\mathrm{kg} \times \mathrm{km}^{-2}$ on the south shore of the St. Lawrence River where wolves had been extirpated at the turn of the century strongly supported this hypothesis.

In the present study, we calculated a standing deer biomass of 95 kg × km^{-2} in the range of the migratory herds of caribou in northern Canada, and of 62 kg × km^{-2} in the moose range shared with established wolf populations in southern Canada. We excluded Alaska (123 kg × km^{-2}) and Yukon (39 kg × km^{-2}) in these calculations because the pronounced relief makes it difficult to delineate the limit between the boreal forest and the tundra, and consequently between caribou and moose range. In the rest of the moose range where wolves were absent or very rare, we measured 299 kg × km^{-2}; deer biomass was particularly elevated in Newfoundland with 457 kg × km^{-2}.

Our data relative to the caribou and the moose range support our prediction and suggest that wolf predation regulated deer in the boreal and mixed forests of North America. Messier and Crête (1985) showed that wolf predation was density-dependent at low moose density ($< 0.5 \times$ km^{-2}), which makes it a potential regulatory mechanism. Crête (1987) also noted that unexploited moose population appeared trapped at low density only when gray wolves coexisted with black or grizzly bear. For instance, moose biomass exceeded 1000 kg × km^{-2} in some years on Isle Royale (McLaren and Peterson, 1994), in the presence of wolves only. Moose have reached similar densities on the south shore of the St. Lawrence river (Crête and Manseau, 1996) and in Newfoundland in the presence of black bear only. Messier (1994) suggested that the presence of a bear species may be necessary for wolves to regulate moose at low density because bear predation on calves reduces the potential rate of increase of moose populations, enabling wolves to numerically respond without delay to changes in moose numbers.

We predicted that deer abundance would vary in relation to forage availability south of the wolf range. As there exists no distribution map of forage availability to deer, we used annual actual evapotranspiration (AE) as a proxi for food abundance (USSR National Committee for the International Hydrological Decade, 1977). Rosenzweig (1968) showed that AE is linearly related to primary productivity for a wide range of ecosystems. We found a significant relationship between deer biomass × km^{-2} (ln-transformed) and AE (Fig. 4; $r^2 = 0.39$; d.f. = 50; $P < 0.0001$); highest standing deer biomass and highest AE values coincided in the south-east portion of the continent. Currie (1991) showed that tree richness was also closely related to AE. We found a stronger relationship between standing biomass of deer (ln-transformed) and tree richness (Currie, 1991: Fig. 1A) than with AE: $r^2 = 0.48$; d.f. = 50; $P < 0.0001$). Our results indicated a poor relationship between species richness and primary production; all five North American deer occurred in some mountainous jurisdictions of the north-west where AE reaches intermediate values, whereas only white-tailed deer were present in the most productive Southeast. This lack of relationship matches the findings for other mammals (Currie, 1991).

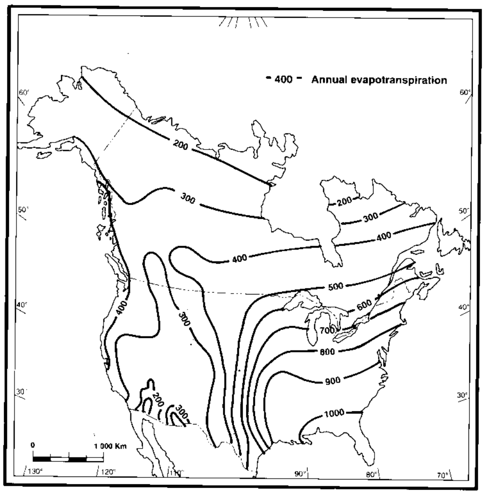

Fig. 4. Annual actual evapotranspiration (mm) for North America (USSR National Committee for the International Hydrological Decade, 1977)

Our results suggest that deer consume a relatively constant fraction of the primary production of an ecosystem. The relationship between standing deer biomass and our gross index to forage availability (AE) probably exists because large herbivores capture most of the energy in an ecosystem (Silva and Downing, 1995); deer represent the dominant family of large herbivores in most landscapes of North America. We must emphasise that our measure of deer abundance also represented a gross estimate. We computed averages over total areas of each jurisdiction without correcting for significant factors like areas of urbanisation, agricultural lands and the nature of farm crops. Such variables may explain the existence of some outliers.

The increase monopolisation of ecosystem energy by deer in the absence of large predators may pose a problem of conservation for plant species consumed by deer (Miller et al., 1992) and of competition with smaller herbivores and their predators. These problems may have been overlooked up to now, and should encourage deer managers to increase harvest pressure on overabundant deer populations. On the other hand, the pattern of deer distribution we observed on the continent allows us to predict that deer abundance will significantly decrease in the north-west United States where introduced and recolonising gray wolves have been rapidly expanding in recent years (Bangs and Fritts, 1996; Pletscher et al., 1997) if managers allow a natural equilibrium to establish between wolves and their prey. The equilibrium biomass of deer should exceed that observed in the moose range (62 kg × km^{-2}), because there are many deer species in this part of the continent, and equilibrium density appears higher in multi-species assemblages than when wolves prey on only one deer species (Crête, 1987; Crête and Manseau, 1996). Multitrophic-level models based on classical predator-prey models (Rosenzweig, 1971, 1973) predict stepwise accrual of trophic level biomass with increasing food chain length (Oksanen et al., 1981; Oksanen, 1988). A fourth functional trophic level could appear with increasing productivity although it is less probable in terrestrial ecosystems (Oksanen et al., 1981); in such a situation, predation and competition between predator species would become high, relaxing pressure on herbivores whose abundance would be set by forage availability. It is possible that such a situation occurred in the most productive parts of North America before European colonisation of the continent. In such a case, plant species growing in very productive ecosystems would have evolved under high browsing pressure by deer for a long period; otherwise the extirpation of predators has imposed an unprecedented high browsing pressure on plant species consumed by deer.

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