Reconstructing Changes in Abundance of White-tailed Deer, *Odocoileus virginianus,* Moose, *Alces alces,* and Beaver, *Castor canadensis,* in Algonquin Park, Ontario, 1860-2004

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The history of White-tailed Deer, *Odocoileus virginianus,* Moose, *Alces alces,* and Beaver, *Castor canadensis,* in Algonquin Park since the1860s is reviewed and placed in the context of changes to the forest, weather, and parasitic disease. Deer seem to have been abundant in the late 1800s and early 1900s whereas Moose were also common but less so than deer. Deer declined through the 1920s as Moose probably increased. Deer had recovered by the 1940s when Moose seem to have been scarce. The deer population declined again in the 1960s, suffered major mortality in the early 1970s, and has never recovered; deer are essentially absent from the present day Algonquin landscape in winter. Moose increased steadily following the decline of deer and have numbered around 3500 since the mid-1980s. Beaver were scarce in the Park in the late 1800s but recovered by 1910 and appear to have been abundant through the early 1900s and at high numbers through mid-century. The Beaver population has, however, declined sharply since the mid-1970s. These changes can best be explained by the history of change to the structure and composition of the Park's forests. After extensive fire and logging in the late 1800s and early 1900s, the forest is now in an essentially mature state. Weather and parasitic disease, however, have also played a role. These three species form the prey base of Algonquin's Wolves, *Canis lycaon,* and the net decline of prey, especially deer, has important implications for the future of wolves in the Park.

Key Words: Algonquin Park, Moose, *Alces alces,* Deer, *Odocoileus virginianus,* Beaver, *Castor canadensis,* Wolves, *Canis lycaon,* ticks, *Dermacentor*, Ontario.

The biota of Algonquin Provincial Park, Ontario, have been under study since the mid-1930s and much information on fish and wildlife resources has accumulated since that time. There are, in addition, anecdotal records of the Park's major fauna from as early as the 1860s. There are particularly useful, if at times sporadic, data on White-tailed Deer (*Odocoileus virginianus*), Moose (*Alces alces*), and Beaver (*Castor canadensis*). Fluctuations in abundance of these species can be related to long-term change to structure and composition of the Park's forests which, in qualitative terms at least, is well known (Strickland 1993). Recently, concern has been raised about the status of Wolves (*Canis lycaon*) in Algonquin Park (Theberge 1998). Moose, White-tailed Deer, and Beaver collectively form the prey of Algonquin's Wolves (Pimlott et al. 1969; Voigt et al. 1976; Forbes and Theberge 1992; Forbes and Theberge 1996) and, ultimately, the fate of the Wolf population will depend on the status of these prey species. This paper is a review of the long-term history of Moose, White-tailed Deer, and Beaver in Algonquin Park.

Methods

The information presented in this paper from prior to about 1940 is essentially anecdotal. Post-1940, the data are from a mix of anecdotal references and population surveys, with formal surveys coming to dominate since about the 1960s. The "historic" information (pre-1940) is largely from land surveyors' reports and annual reports of the Park Superintendent to the Minister responsible for Crown land. Post-1940 the data are from a variety of sources including annual reports of the Department of Lands and Forests (which became the Ministry of Natural Resources (O. M. N. R.) in 1972) which often featured Algonquin Park, unpublished reports from staff who worked at the Park's Wildlife Research Station, and, increasingly with time, published research papers.

From about the mid-1950s the population surveys developed into standardized techniques accepted across the province. For Moose, this involved the gradual application of plot-based mid-winter aerial surveys that began in Ontario in about 1950 and have evolved into a formalized provincial survey technique (Bisset 1996*). The currently accepted technique came into more or less its current form in the mid-1970s, but aerial survey data are reported here from 1950, the earlier surveys being somewhat less rigorous in design.

Epizootics of Winter Tick, *Dermacentor albipictus,* can cause severe die-offs of Moose (Blyth and Hudson 1987). In the early 1980s, E. Addison established a technique to assess the severity of tick infestation by modification of a "hair loss index" first developed in Alberta (Samuel and Barker 1979). The technique measures the extent of hair loss that is apparent on

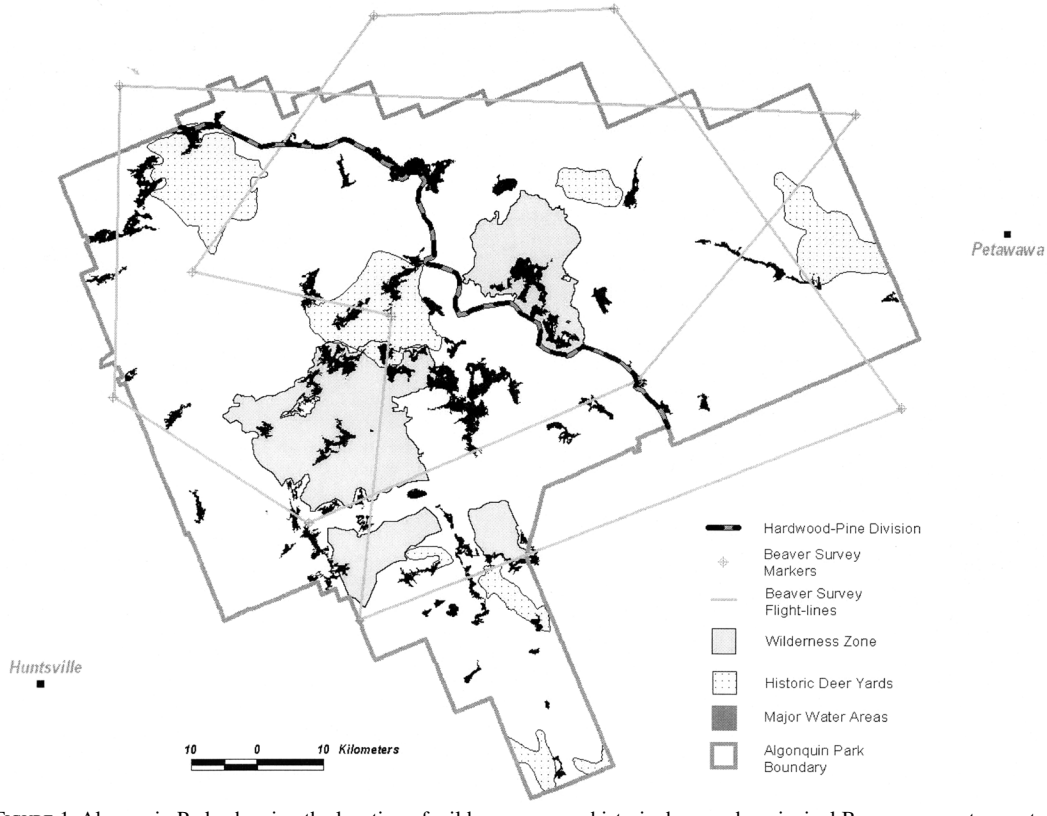


FIGURE 1. Algonquin Park, showing the location of wilderness zones, historic deer yards, principal Beaver survey transects, and the east-west division of forest types.

Moose in late winter. A survey is flown by helicopter on one day from 20-25 March in an approximately 2000-km^2 zone in the south-center of the Park to place at least 40 Moose in the five categories of hair loss proposed by Samuel and Barker. A simple arithmetic index, the Hair Loss Severity Index (H. S. I.), is then calculated by multiplying the number of Moose in each category by its severity rank (1-5), summing this, and dividing by the total Moose observed. The H. S. I. is used to predict the extent of mortality the following spring.

Deer are much more difficult to census than Moose and have generally been surveyed by counting droppings or "pellet groups", a technique that was first employed in the U. S. in about 1940 (Bennet et al. 1940) and came into use in Ontario shortly afterwards. The technique was first applied in Algonquin Park in the mid-1950s and a protocol was developed that was used throughout south-central Ontario into the mid-1970s (Anonymous 1980*). These pellet group surveys provide the best reference to deer populations in the Park. As will be shown, the Park's deer population declined drastically in the early 1970s and the technique, which is difficult in even ideal conditions and unreliable at low deer densities, was abandoned.

Since the early 1970s deer surveys in the Park have consisted of late-winter aerial surveys of historic deer wintering areas ("yards"). Eight deer yards, some greater than 10 000 ha, were located across the Park (Figure 1) and supported high densities of deer (e.g., Stanfield 1957*) through mid-century. Several of these yards were surveyed in each of 1985, 1989, 1994, 2000, 2001, and 2004. Every yard was flown at least once in the years listed and most were flown several times. The 2004 survey included several areas in the south-center of the Park that were outside the historic yards but with potentially good winter cover. The surveys were done in mid- to late March when snow is deepest. North-south transects were flown at 1 km intervals with fixed wing aircraft at approximately 140-km/h airspeed and deer tracks and trails tallied along the transects. In addition, deer sign was recorded during an aerial Wolf survey from 6-23 February 2002 (Patterson et al. 2004). Fifty-one hours were flown in a Bell 204 helicopter at approximately 100 m over 44 5×5 km survey plots. Many of these plots were located in the historic yards and nearly all had at least some coniferous cover potentially suitable for deer.

Since 1955, Beaver have been surveyed in the Park by counting live colonies along aerial survey transects. The surveys have generally been done in late October after leaf fall but before ice-up when Beaver are actively storing food and evidence of fresh cutting (i.e., food piles) can be readily observed from the air. Results have been expressed as live colonies per unit area. There have been several different types of surveys and results of essentially all are reported here. The best data are from a long series of a survey first done in 1960 by Rod Stanfield that consisted of two transects that each formed a circuit around the Park (a short segment of each flight was outside the Park, Figure 1). The survey was flown at a constant height of 800 feet by reference to points of elevation along the transects, and the observers line of sight established through a wing strut so that an observed band of 3200 feet was centered on the transect. Smith (1969*) summarized these data from 1960 – 1968. Stanfield described his survey technique, including the "way points" at the end of each transect, precisely, so that the survey can be repeated accurately. E. Addison reviewed and reinstated the survey in 1998 (Addison 1998*) and the survey was flown again in 1999 and 2003.

Further information on specific survey methodologies can be found in the papers cited above. Unpublished works and much of the original data for surveys referred to throughout this paper are found either in the O. M. N. R. Research Library in Peterborough, Ontario, or the Archives of Algonquin Park.

Winter severity is a key factor in the productivity and survival of deer (e.g., Mech et al. 1987) and very severe winters can result in mortality of Moose (Bishop and Rausch 1974). Historic records of winter weather are presented and related to trends in abundance of deer. Monthly means of temperature were obtained from the Ontario Climate Center of Environment Canada in Downsview, Ontario, for Algonquin Park (Park Headquarters at Cache Lake) from 1917 to 1972 and Dwight, Ontario, from 1973 to 2002 (the weather station was closed in the Park in 1973; Dwight is 20 km west of the Park boundary). Snow accumulation was obtained from a snow depth station that has been operating at the Park's west gate since 1952.

Forest management is also a key influence on all three species (e.g., Monthey 1984; Novak 1987; Peek 1998). An overview of the history of logging and fire suppression in the Park is given in the next section before results of the various surveys are presented.

Results

History of Logging and Fire Suppression

Algonquin Park is 7600 km^2 and is a multiple-use Park consisting of a complex array of zones in which varying degrees of activity are permitted. Complete protection is afforded to Wilderness Zones (Figure 1) but commercial logging is permitted in the Recreation-Utilization Zone, which comprises 78% of the Park. However, with various reserves of land for, for example, shoreline protection, only about ⅔ of the landbase is available for logging. This zoning system was established in the Master Plan of 1974 (Anonymous 1974*) and has been affirmed by Management Plans since then (Anoymous 1998*).

The Park actually consists of two forests; the eastern third of the Park consists essentially of pine forests, primarily White Pine, *Pinus strobus,* with lesser amounts of Red Pine, *Pinus resinosus,* and isolated Jack Pine, *Pinus banksiana,* stands on well-drained, sandy outwash and rolling to flat terrain. The remaining two thirds, approximately 4600 km^2 of the Park's west side, consists of tolerant hardwood forest: Sugar Maple, *Acer saccharum,* American Beech, *Fagus grandifolia,* Yellow Birch, *Betula alleghaniensis,* and Hemlock, *Tsuga canadensis,* on glacial till over poorly-drained rugged terrain (Figure 1).

As early as the 1830s (Strickland 1993) loggers entered the Park seeking White and Red pine "square timber" coincident with the removal of pine across northeastern North America at the time (Runkle 1985; Abrams and McCay 1996). Logging progressed rapidly up the main waterways of the Park; by 1866-67, 30 000 pieces of square timber were removed annually (Strickland 1993). The square timber activity had peaked about 1864 and declined thereafter, the last square timber being cut in 1912 (Anonymous 2000*). White Pine, however, remained the focus of interest as sawmills appeared before the square timber period ended.

It seems that the removal of pine was extensive, nearly complete in places. Recent work analyzing remnant pine stumps (the fine remains of which can persist more than 120 years) suggests that 70 – 94% of the pine was removed from hardwood forests in the south-center of the Park (Simard 2001). The debris left from this logging fostered extensive fires primarily in the east-side pines (Fitzgerald 1890*, and see historic notes in Runge and Theberge 1974). Fires were frequent into the early 1900s although Superintendent G. W. Bartlett noted in several of his annual reports that these fires were "generally brought under control" (Bartlett 1905-1921*).

By the 1930s attention turned to hardwoods, in part because the pine had been depleted but also because of the development of new markets, including Yellow Birch veneers for construction of the Mosquito fighter-bomber of World War 2 (Anonymous 2000*). Remnant stands were often logged over for pulp (Runge and Theberge 1974). Fire apparently remained common until the early 1930s (Robinson 1933).

Hard data on the extent of the removal of forest cover from all this activity is lacking but it appears that it was, in places at least, extensive. Photos exist from the late 1800s and early 1900s showing barren hillsides in the Park (Algonquin Park Museum Archives). White-tailed Deer, Moose, and Beaver are fundamentally adapted to early successional habitats (Novak 1987;

Voigt et al. 1997; Peek 1998) and, from the point of view of food supply at least, habitat was probably favourable for all three species through the first half of the 1900s. Hall (1971), for example, noted that by 1893 the logging of White Pine in Algonquin Park had been underway for 50 years and "considerable areas of the Park were undoubtedly in the secondary stages of forest succession that provide good beaver habitat". Stephenson and Hepburn (1958*) reported that continued logging since the 1800s had brought a "succession of areas" into a good productive state for deer.

The harvest of Yellow Birch was gradually supplanted by Sugar Maple, the primary use of which has shifted over time from sawlogs to pulp (Anonymous 2000*). Hemlock, which is excellent winter cover for deer (Voigt et al. 1997), was not a priority species historically, nor is it today, but it was harvested in the late 1800s and early 1900s in the southwest of the Park for the tan bark industry (Strickland 1993) and then extensively in the 1960s for shoring timber, principally to build the Toronto subway (Wilton 1987). Wilton reported that 203 456 acres (82 339 ha) were cut over in six of the historic deer yards in the Park from 1952-1971. He pointed out that, although this created regeneration for browse, "large volumes" of coniferous cover, particularly of Hemlock, were removed to the detriment of deer (Wilton 1987). M. Robinson made the same point in 1933, suggesting that "many of the former yarding grounds have been destroyed by lumbermen removing the spruce, pine, and hemlock" (Robinson 1933).

As early as the late 1930s (Runge and Theberge 1974) and definitely by the early 1950s (Anonymous 2000*) diameter limit harvesting began to replace the more or less unregulated cutting. This evolved into partial cutting systems; the single-tree selection system, which was first employed in the late sixties in the hardwoods, and "uniform shelterwood" harvest in the pine stands on the east side.

Selection cutting, which has been applied across the western ⅔ of the Park since the 1960s (Strickland 1993; Anonymous 2000*), retains a more or less intact forest canopy. Partial cutting systems can produce a considerable shrubby understory (Kelty and Nyland 1983) that is frequently renewed because stands are "treated" every 20-25 years. However, selective logging does not produce the biomass of browse that more aggressive logging systems do (e.g., Monthey 1984) and biologists in Ontario do not consider it of optimal benefit to browsers like deer (Voigt et al. 1997). Research on the effects of pine uniform shelterwood on ungulates is lacking but the system is normally effective at regenerating White Pine (Anonymous 2000*) that grows to dominate the understory and thus may not produce large quantities of palatable browse.

Forest fire is not normally active in mature tolerant, or "Northern", hardwood forest found on the Park's west side (e.g., Lorimer and Frelich 1994) and must have become less frequent as the forest recovered. Fire, on the other hand, is naturally very frequent in the Park's east side pines (Cwynar 1978). Fire was, at any rate, gradually eliminated from the landscape more or less coincident with the shift to low-impact logging. The introduction of fire towers and "fire ranging" aircraft in the late 1920s began a process that rapidly brought down the area of forest burned annually (Runge and Theberge 1974). Forest fire has been under essentially complete control in the Park for decades; although there are approximately two dozen lightning "starts" each year, fires rarely get past one hectare in size (Anonymous 2000*).

Today, as a result of the elimination of fire and evolution to selection logging, the Park's forests are in an essentially mature state. Seventy-seven percent of the Park's hardwood zone is in mature tolerant hardwoods and the rest is in "static" wetland (e.g., Black Spruce, *Picea mariana*) or swamp hardwood forest, or mature intolerant hardwoods that are succeeding to Maple-Beech (Quinn 2004). The east-side pine forests are also primarily mature or uneven-aged (Anonymous 2000*). The 22% of the Park that is in protected zones and has not been logged since at least the 1960s is also essentially mature forest, and, in places, approaching "old growth" (as defined by Keddy 1994 and Tyrell and Crow 1994).

In summary, the Park's forests were extensively disturbed in the late 1800s and early 1900s but recovery began in the 1930s with the suppression of fire and adoption of low impact logging techniques. It is widely accepted that the recovery of the Park's forests has been detrimental to both White-tailed Deer (Runge and Theberge 1974; Wilton 1987) and Beaver. Moose have, as will be seen, increased through at least the later part of this period.

Trends in Populations

Deer

The presettlement distribution of ungulates in central Canada is poorly understood, largely because bone deteriorates rapidly in the acidic soils of the Canadian Shield (Reid 1988). It is widely believed, however, that prior to European contact and the opening of the forests, deer did not range in Ontario north of approximately the location of Hwy 7, which is approximately 160 km south of the center of the Park (Matheson 1972; Smith and Borczon 1977; Smith and Verkruysse 1983). Deer bones were found in a dig of native hearths near Whitson lake in Algonquin Park but could not be reliably dated and were presumed to be post-settlement (Burns 1972*).

The earliest published evidence of deer in Algonquin Park is that of R. Bice in Wilton (1987) who reported that deer were found in the Park from at least the 1860s. There are a series of land survey records that suggest that White-tailed Deer (and Moose) were abundant in Algonquin through the late 1800s. Typically, the sur-

veyors noted that "the woods abound with moose and red deer" (Dickson 1883*; Byrne 1884*) or "red deer and moose roam all over the country" (Fitzgerald 1890*). There is, however, one dissenting voice in 1887; "little, if any, game was seen during the survey" (White Township.) (Fitzgerald 1887*).

From 1905 to 1921, G. W. Bartlett, Park Superintendent, wrote annual reports on Algonquin Park to the Minister of Lands and Forests. These reports consistently suggest that deer were very abundant. Phrases like "the deer are here simply in thousands and … increasing" are found throughout (e.g., Bartlett 1907*). In 1911 Bartlett reported that "deer are so abundant they can be seen from the hotel veranda in numbers" and in 1910 that deer supported great hunting on the Park's boundaries and that "the Park is a great feeder for the surrounding country".

Robinson (1933) reported that deer numbered in the tens of thousands in 1921 but had declined to "possibly not more than three thousand" by 1933. Although there are no snow depth records for the time, winter temperatures were not unusually cold, indeed rather warm for the late 1920s – early 1930s (Figure 2). Robinson in fact emphasized deteriorating habitat, in part because of the suppression of fire, as the cause of the decline (Robinson 1933). The population, however, apparently recovered because C. H. D. Clarke reported a "chronic overpopulation" of deer in 1945 and reports an estimate of 13 deer/square mile, from a very early pellet group survey, a number he considered "suspiciously low" (Clarke 1945*). A. Leopold also listed the Algonquin deer population as among those "overpopulated" in North America at the time (Leopold et al. 1947).

Population estimates from pellet group surveys began to appear regularly in the 1950s. Stephenson (1958*), for example, estimated 53 deer/square mile in a wintering yard (where, of course, deer were concentrated) in Biggar Township in 1957. He was researching means to ameliorate "heavy cropping" of Yellow Birch by deer at the time (Anonymous 1957*, see research section page 72) so deer must have been abundant. Estimates from pellet group surveys for the area around Swan Lake, in the southwest corner of the Park suggested 15 deer/square mile in winter and 12 in summer in 1957 (Stephenson and Hepburn 1958*). Estimates of 12 deer per square mile would have put the Park population at approximately 36 000 animals at the time.

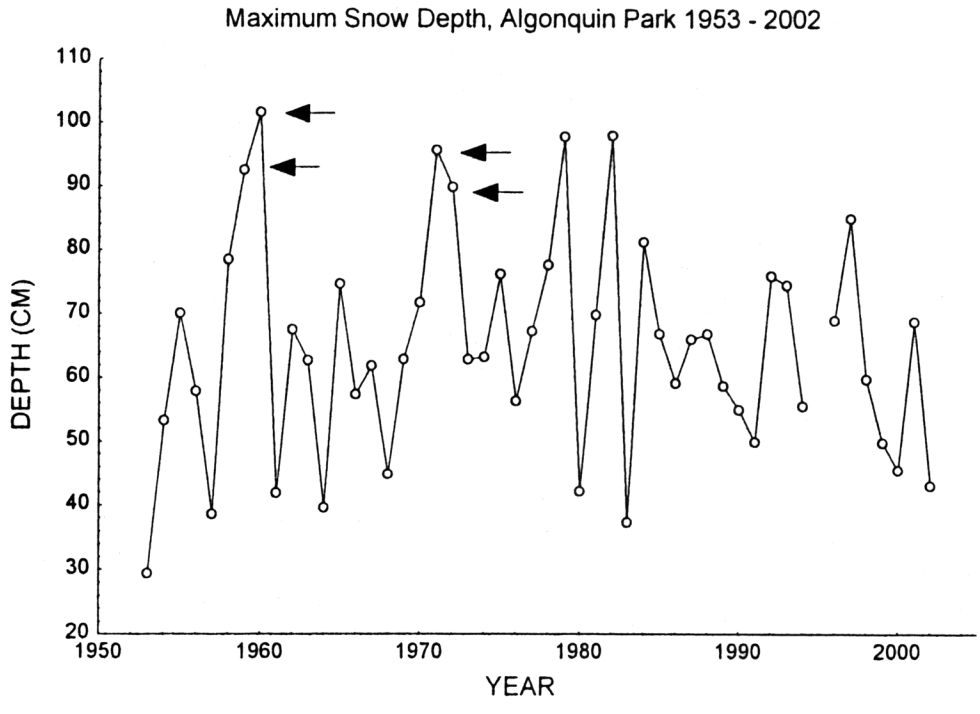
There was apparently significant winter mortality (a "die-off") of deer in the winters of 1958-1959 and 1959-1960 (Runge and Theberge 1974). These winters were indeed cold and snow accumulation was exceptional (Figure 2). The range was also overbrowsed at the time; Grant Taylor, retired Park naturalist, recalls that all regeneration from ground to five feet in height was browsed (G. Taylor, personal communication). The losses, however, may not have been extensive because there is an estimate of 69 deer/square mile in a yard in the Kiosk area in 1961 (Anonymous 1961*) and deer are reported to have "recovered" by 1965 (Anonymous 1965*). B. Stephenson reported 10 deer/mile^2 in summer within a 3 square mile study area located in the south of the Park in 1960 (Pimlott et al. 1969, page 29). Deer must have been common in the Park in the 1960s because the late Roy Anderson reported having "hundreds" of road-killed deer to dissect for his studies of meningeal worm, *Parelaphostrongylus tenuis*, in the 1960s (R. Anderson, University of Guelph, personal communication).

Notwithstanding this, deer apparently declined gradually through the 1960s (Rutter 1964; Runge and Theberge 1974) and this culminated in a severe die-off in the winters of 1970-1971 and 1971-1972. Wilton (1970*) estimated a population of 8090 in 1970 but that had declined to 2800 by 1972 (Wilton and Trodd 1972*). The decline was also documented in King (1976) who reported extensive mortality of deer in central Ontario in the winter of 1970-1971 and a density of only 2.02 deer/square mile in Pembroke District (which included Algonquin Park) in spring of 1972. King attributed the decline to winter severity, and snow depths were indeed exceptional (Figure. 2). Snow was also persistent those two winters; the peak of snow depth in Algonquin Park is normally the second week in March but it was mid-April in 1971 and late March in 1972.

The sharp decline of deer that occurred in Algonquin in the early 1970s happened throughout central Ontario (King 1976). Deer populations have since recovered around the Park but the Algonquin population never recovered. Deer are fairly common in the Park in summer; Park staff have been conducting road counts since 1999 and one deer is seen per approximately 270 km driven on Hwy 60 in May (roughly one deer per eight Moose, unpublished data: Algonquin Park files). However, deer are very scarce in winter. Essentially no deer or deer tracks were seen in any of the aerial deer yard surveys from 1984-2004 described earlier (including the 2002 Wolf survey). The only exception to this is the yards in the Southern "panhandle" (Figure 1) which still support deer. Deer or deer tracks are also rarely observed during winter aerial Moose surveys of the Park.

Moose

Moose were almost certainly on the early Algonquin landscape. Moose are known to have existed in Maine in the 1600s and in Quebec at the same latitude as Algonquin Park in the 1500s (Reeves and McCabe 1998). Furthermore, Peterson (1955) suggests that Algonquin Park was within the range of Moose in 1875. Intriguingly, however, it was noted in the Royal Commission Report on the founding of the Park in 1893 that Moose were unknown to the Indians prior to 1870 when they made their first appearance "at least



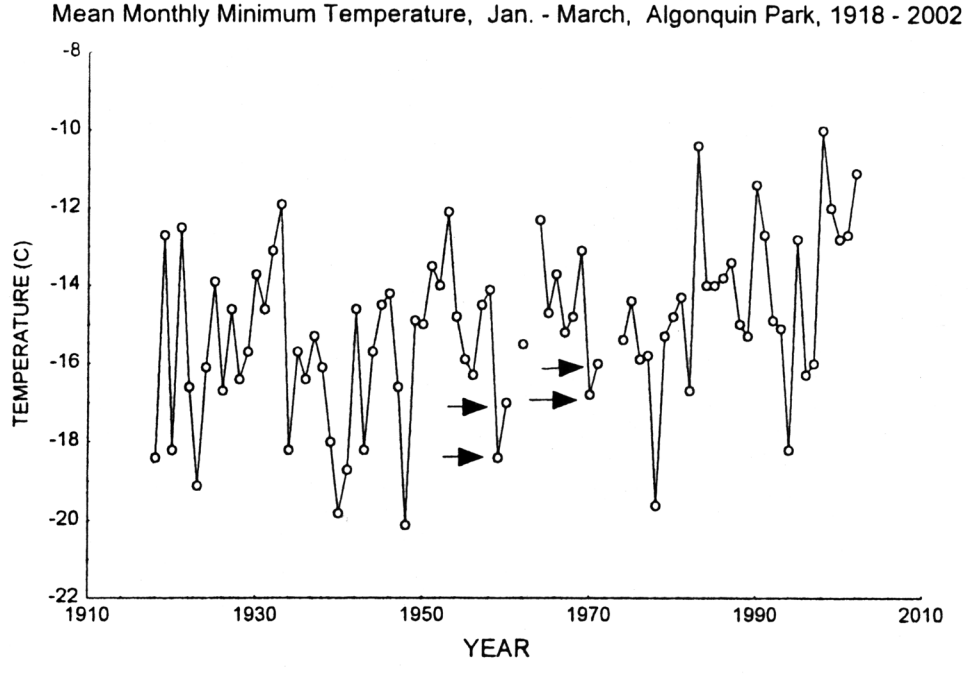


FIGURE 2. Long term trends of snow depth and winter temperature in Algonquin Park. Arrows point to years of deer die-offs.

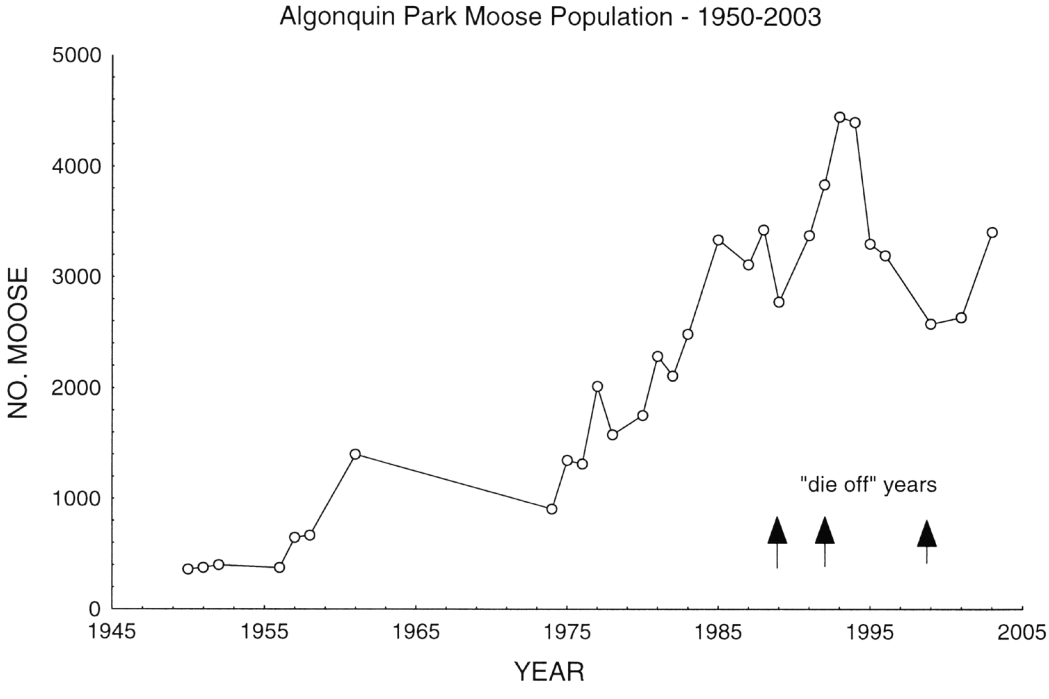


FIGURE 3. Moose population estimates, Algonquin Park, 1950 – 2003.

in recent times" after crossing over from Quebec (Anonymous 1893*).

Moose were, at any rate, well established in the Park by the late 1800s as evidenced by reports of the early land surveyors (e.g., Dickson 1883*; Byrne 1884*; Fitzgerald 1890*) discussed earlier. Reports of wasteful killing of Moose by hunters in the late 1800s in the area soon to be Algonquin Park (Anonymous 1893*) also suggest high numbers. Bartlett's annual reports, however, suggest that Moose were less common than deer in the early 1900s (Bartlett 1905-1921*). Moose are consistently referred to as "increasing" or "greatly increased" but as secondary to deer in these reports. Moose may, however, have been locally numerous as "in great numbers along the Nipissing River" in 1908 (Bartlett 1908).

There is a gap in reports of Moose abundance through the 1920s and 1930s, although Robinson (1933) reported that Moose "have increased greatly in numbers" after the "disappearance of the deer" he had noted from the early 1920s; the implication is that Moose were scarce relative to deer up to about 1921 which is in agreement with Bartlett. It seems, however, that Moose had declined again by the 1940s. Robb (1942) reports seeing only 19 Moose (but 254 deer) in Beaver surveys in the Park in 1939-1940 and C. H. D. Clarke suggested that Moose were very scarce in 1945. Clarke reported that although Moose are "distributed across the Park" only "one specimen found dead"'could be examined and that "Algonquin Park is hardly the place to study moose in Ontario" (Clarke 1945*). He further reported that only two Moose pellet groups were found in 98 deer pellet group plots.

Population estimates for Moose post-1945 are shown in Figure 3 and show a more or less steady increase until the present. Estimates in Figure 3 post-1985 are directly from the Park's data files; those prior to 85 are from DeVos (1952*); Pimlott et al. (1969, page 32); Wilton and Pashuk (1983*) (to which the 1984 and 1985 estimates were appended); and several Department of Lands and Forests annual reports from 1954-1968. The population estimates from 1956-1958 are extrapolations from estimates of Moose density for Pembroke District (which included Algonquin Park). Also, as few as 12 plots were used in some of these early surveys so they may not have been very accurate. Years missing in the inventory post-1974 are the result of poor survey conditions.

The late March survey of winter tick induced hair loss was done 14 times from 1984 to 2004. The mean H. S. I. was 1.90 (range 1.18 – 3.48) and there was evidence of heavy losses of Moose in spring following three of five surveys (March of 1989, 1992 and 1999) in which the index was > 1.95. Moose carcasses, or the stench thereof, were frequently reported by the public throughout spring of 1989 and 1992 (personal obser-

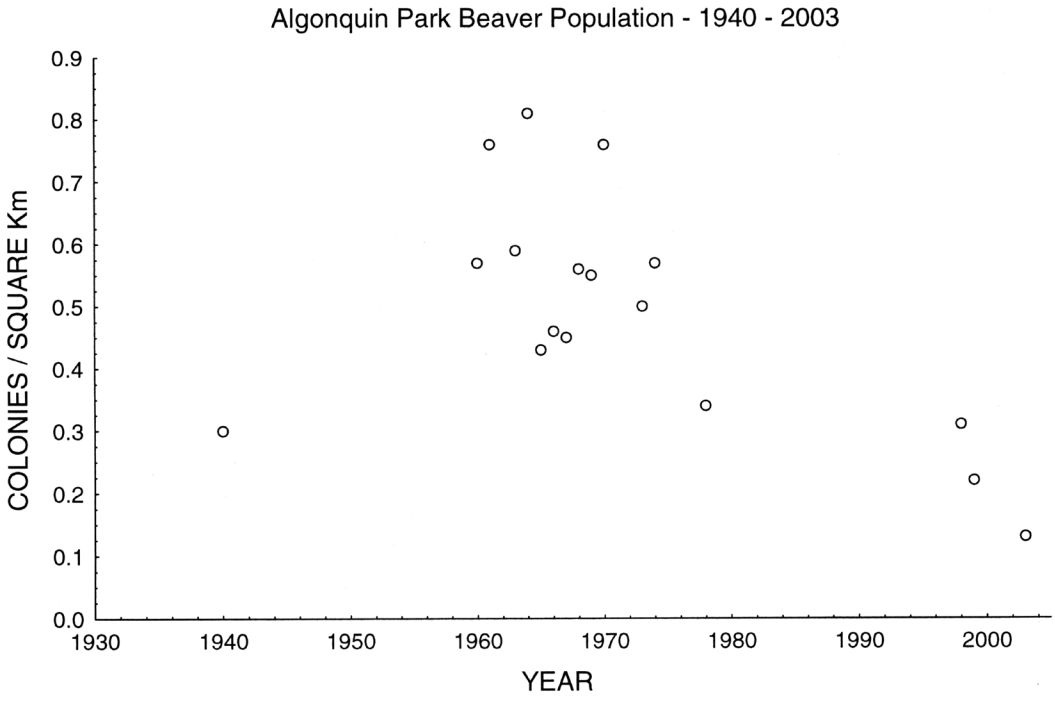


FIGURE 4. Beaver population estimates, Algonquin Park, 1940 – 2003.

vation). In 1999 (while I was on leave) the H. S. I. reached its highest and there was evidence of extensive mortalilty (B. Sandilands, Park Planner, personal communication). Unfortunately, aerial Moose surveys in two of the three winters following this apparent heavy mortality (1990 and 2000) were cancelled or only partly completed and thus the population effects are unclear [and note that the survey in winter of 1993 actually showed an increase (Figure 3)].

Beaver

There is little about Beaver from the early land surveys except a reference from 1890 about scattered Beaver meadows "now more or less dried up" (in White Township) (Fitzgerald 1890*). James Dickson Provincial Land Surveyor, however, wrote in 1888 that trapping had greatly reduced the Beaver population in the region soon to become Algonquin Park and Peter Thompson, first Park Superintendent, reported that "scarcely a beaver could be seen" (Hall 1971). By 1899, however, the Beaver population had reportedly recover-ed and were so numerous by 1909 that the Park Superintendent recommended that trapping (which had been suspended) be reinstated (Hall 1971). Superintendent Bartlett's reports suggest that Beaver flourished from 1905-1921. In 1906, for example, Bartlett wrote that "fur bearing animals have greatly increased, especially the beaver". Bartlett reported in 1908 that "the beaver can be found in numbers upon every lake, river, pond and creek" and in 1909, "in large healthy colonies wherever there is a drainage ditch" (he lamented the extent of "nuisance" problems Beaver were causing in the 1908 report). The remaining reports frequently note Beaver increasing, for example "the annual increase of which (Beaver) runs into the thousands" in 1919.

Information is lacking for the Park for the 1920s. However, Beaver were apparently plentiful across the province up until 1923 but declined sharply (province-wide) in 1924 and remained low, and of concern, until 1930 (Anonymous 1923-1930*). No reason is given for the decline and it is not clear if the decline occurred also in Algonquin Park.

Robb (1942) reported a density of 0.29 Beaver colonies/km^2 in 1940 in the south-center of the Park but Hall (1971) believed that Robb underestimated the population and reported that Beaver populations had fluctuated between 0.40 – 0.80 colonies/km^2 from 1955 to 1971. Beaver must have been relatively abundant in the 1950s because R. Stanfield reported an "unusually high density" in 1955 and between 58 and 77 colonies/100 "bodies of water" in 1957 and that this was high "relative to all other Districts except North Bay" (Stanfield 1957*).

Population density estimates of Beaver (colonies/km^2) for the Park from 1940 to 2003 are shown in

Figure. 4. These data are primarily Stanfield's survey [summarized in Smith (1969*)] and its recent continuation (Addison 1998*), but include several other independent estimates (Robb 1942; Wilton 1974*; Regan 1978*). The data suggest that the Beaver population has declined sharply since the late 1970s (Figure 4). This is reflected in independent studies in the south-center of the Park by J. Fryxell, who reported a significant 50% decline of Beaver from 1987-1998 (Fryxell 2001).

Discussion

In summary, White-tailed Deer appear to have been common in Algonquin Park in the late 1800s while Moose were present but secondary to deer. Deer remained abundant and apparently increased through the early 1900s until a decline from the early 1920s to the early 1930s. Deer had recovered by the early 1940s and were common through the 1950s but began to decline in the 1960s and suffered severe losses due to winter severity in the early 1970s and have not recovered. Moose were apparently secondary to deer in the early 1900s and probably relatively scarce until the decline of deer in the 1920s when they are reported to have increased. By the 1940s, however, Moose had declined (coincident, apparently, with the recovery of deer) and appear to have been quite rare by the mid-1940s. Aerial surveys show an increase in the Moose population beginning in the mid-1950s that accelerated with the decline of deer in the early seventies. Moose are now the dominant ungulate in what was a Wolf-deer system through most of the last century. Beaver were scarce until the formation of the Park in 1893 whereupon they increased rapidly and were very common through the early 1900s. There are little data on Beaver until aerial surveys first began in 1940. Surveys and qualitative assessments suggest that Beaver were abundant and more or less stable at about 0.5 colonies / km^2 through mid-century but began to decline in the mid-1970s and are now at less than half of their peak abundance.

The conventional explanation for the observed trends in White-tailed Deer and Moose is that the removal of coniferous cover and gradual maturation of the forest have been detrimental to deer and, consequently, of benefit to Moose (Robinson 1933; Runge and Theberge 1974; Wilton 1987). Presumably, maturation of the forest also accounts for the decline of Beaver (Addison 1998*). The system, however, is more complex than just that and a more detailed discussion is in order.

The opposition of Moose and deer numbers over time is intriguing given the potential virulence of meningeal worm to Moose (Anderson 1964). Meningeal worm is widely distributed in eastern North America and present in Algonquin Park and one is tempted to conclude that Moose increased in the Park as deer, and the rate of transmission of *P. tenuis,* declined. Wildlife managers in the Park and elsewhere have assumed this effect occurs, at least with relatively high deer densities (e.g, Karns 1967). However, the ecological role of meningeal worm is poorly understood and evidence for the degree of its impact on Moose has been challenged (Nudds 1990). Nevertheless, the parasite must remain implicated as having a potential role in the recurring divergence of Moose and deer numbers in the Park.

There are other enigmatic questions regarding Moose and White-tailed Deer. For example, the scarcity of deer in the Park in winter while deer are abundant all around the Park is hard to explain. It is, as discussed, widely believed that this is a result of the deterioration of habitat in the Park but also because winter weather is more severe than for the surrounding landscape. The latter is true; for example mean monthly minimum temperatures in winter are lower in a zone centered on the core of the Park than the surrounding area (Anonymous 1984). Yet deer winter in large numbers in yards almost adjacent to the Park boundary where winter weather is only marginally different. For example, deer winter in the hundreds in yards near Dorset (J. MacDonald, O. M. N. R., Bracebridge, personal communication) only 15 km from the Park boundary and at 1100 m elevation vs 1250 m for Hogan Lake, one of the original yards in the Parks's core. The structure and composition of the forest around Dorset and the surrounding landscape, is, superficially at least, similar to that of the Park (personal observation). Why, then, are deer so scarce in the Park in winter?

Wolves may be the answer to this question. We occasionally find Wolf-killed deer in the Park in mid-winter in places where their presence was not previously obvious. In the 2002 aerial Wolf survey one of only four deer observed was a recent Wolf kill and a second was being pursued by Wolves. It seems that Wolves are very effective at finding the few deer that do winter in the Park (Forbes and Theberge 1996). Possibly, White-tailed Deer have not been able to reoccupy the Park after the die-offs of 1971 and 1972 because Wolves have essentially excluded them (at least in winter). There is in fact a body of evidence that predation is disproportionately heavy on isolated groups of deer wintering away from the core of large yards (Kolenosky 1972; Nelson and Mech 1981; Patterson and Messier 2000).

Another aspect of this question is the effect on deer of supplemental feeding around the Park in winter. Deer on the Park's east side are known to migrate out of the Park in winter to areas to the southeast where supplementary feeding is widespread (Forbes and Theberge 1995). Supplementary feeding occurs around much of the Park and has for decades, but became commonplace after the decline of 1970-1972 (M. Wilton, O. M. N. R, retired, personal communication) (it is not practised in the Park). Deer exhibit strong philopatry and will bypass good quality habitat to

winter in hereditary yards even where quality of habitat is poor (Voigt et al. 1997). Possibly, supplementary feeding has, over time, created a fixed "culture" of seasonal movement out of the Park. Lewis and Rongstad (1998) showed that supplementary feeding of deer can influ-ence migration.

One hypothesis, then, to explain the recent history of deer in Algonquin Park is as follows: The decline of deer in central Ontario in the early 1970s was particularly severe in Algonquin Park. Deer recovered around the Park but were slower to do so in Algonquin because of poorer quality of habitat and somewhat more difficult winters. Supplementary feeding, which began in earnest shortly after the decline of deer, presented a draw that developed into fixed winter migrations and the few deer that try to break that mode are killed by Wolves.

Moose also present a dilemma. With the exception of some island populations in northwestern Ontario, Algonquin Park has supported the highest Moose population density in the Province for years; typically showing densities three times higher than in northern management units (O. M. N. R., Wildlife Surveys and Records). The Park, however, is almost the antithesis of good Moose habitat. Quality Moose habitat is traditionally viewed as landscapes that are extensively disturbed; boreal forests with a mix of burns and/or clearcuts amidst winter cover and aquatic feeding areas (e.g., Peek 1998). Algonquin Park, or at least its western two thirds where Moose densities are highest, is a closed-canopy tolerant hardwood forest with very few openings larger than a few hundred square meters (Anonymous 2000*; Quinn 2004). Fire has not been active on the Alqonquin landscape for decades and, even when not suppressed, is very rarely a stand destructive event in tolerant hardwoods (Lorimer and Frelich 1994). Partial cutting systems in hardwoods can provide substantive browse (Kelty and Nyland 1983) but much less than clearcuts (Monthey 1984). Why, then, are there so many Moose in the Park?

Here, again, the answer may lie in predation for, on the Park's west side at least, there is no effective predator acting on Moose. Hunting by a local aboriginal community is permitted on the east side of the Park in a zone corresponding roughly to the extent of pine forest (about 40% of the Park's area). The west side (hardwood) area is, however, unhunted. Further, Algonquin's Wolves, although capable of killing Moose, are principally a "deer-eating" type (Pimlott et al. 1969), and primarily a scavenger of Moose in winter (Forbes and Theberge 1992, 1996). A hypothesis regarding the Algonquin Moose population thus goes as follows: Moose are at high densities in Algonquin Park because of the lack of an effective predator, not the quality of habitat. Habitat is marginal but acceptable; selective cutting provides a limited but continuous supply of browse and coniferous cover, while generally unsuitable for deer, is adequate for Moose. Relatively low predation pressure, and very low densities of deer (and thus *P. tenuis*) allow Moose to do well in a forest environment that is not optimal.

A less well understood player in this system is the Black Bear (*Ursus americanus*). Black Bears prey on Moose calves and can limit Moose populations (Stewart et al. 1985). Data on bear predation on Moose calves in Algonquin, however, are sparse. Moose are believed to calve preferentially on islands and peninsulas in the Park to avoid bears (Addison et al. 1990) but Garner (1994) showed a predation rate of bears on Moose calves in the Park of only 8% which is low relative to that suggested by removal studies of Brown Bears (*Ursus arctos*) in Alaska (Miller and Ballard 1992) and Black Bears in Saskatchewan (Stewart et al. 1985).

The Algonquin ecosystem, and particularly the complex interplay of Wolf-prey, habitat, weather, and parasites will continue to evolve and present challenges to Park managers. The future of the Park's Wolves will depend largely on trends of these prey populations. This basic truism has largely been overlooked in the discussion on the status of Algonquin's Wolves which has focused on human killing around the Park as the cause of the possible decline (Theberge 1998). This paper suggests that declining prey may be at least as important a factor. Algonquin's Wolves are small and prey preferentially on deer (Pimlott et al. 1969; Forbes and Theberge 1996). The near absence of deer in winter and decline of Beaver, an important summer food, must be stressful to the population, as has been documented in Minnesota (Van Ballenberghe and Mech 1975). The increase of Moose has in part compensated but Algonquin's wolves are primarily scavengers of Moose in winter (Forbes and Theberge 1996) and may find food energy from Moose readily available only in winters of tick induced mortality.

Algonquin Park, and its wolves and prey, do not exist in isolation. Indeed, recent work suggests that Algonquin's wolves are not unique but genetically identical to and freely interbreeding with wolves around the Park (Grewal 2001). The larger population, a distinct taxon, the "Eastern Canadian Wolf", *Canis lycaon,* (Wilson et al. 2000) extends from Manitoba to Quebec and numbers approximately 10 000 (Van Zyll de Jong 1996*; White et al. 2001*). External phenomena that are both minor and local, like feeding deer, and great and global, like climate change, will perhaps have as much influence on future trends in the distribution and abundance of *C. lycaon* as changes within the Park itself.

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