MOOSE AND DEER POPULATION TRENDS IN NORTHWESTERN ONTARIO: A CASE HISTORY

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ABSTRACT: Many interrelated factors contribute to the rise and fall of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) populations in the mixed boreal forests of eastern North America where these species often cohabit. A question not satisfactorily answered is why do moose populations periodically decline in a pronounced and prolonged way while deer populations continue to do well during times when habitat conditions appear good for both? Long-term historical data from the Kenora District of northwestern Ontario, Canada provided an opportunity to better understand temporal relationships between trends in deer and moose numbers and landscape-level habitat disturbances, ensuing forest succession, climate, predators, and disease. Over the past 100 years, moose and deer have fluctuated through 2 high-low population cycles. Deer numbers were high and moose numbers were low in the 1940s and 50s following a spruce budworm (*Choristoneura fumiferana*) outbreak. By the early 1960s, deer trended downwards and remained low during an extended period with frequent deep-snow winters; as deer declined, moose recovery was evident. Moose increased through the 1980s and 1990s as did deer, apparently in response to considerable habitat disturbance, including another spruce budworm outbreak and easier winters. However, despite conditions that were favourable for both species, moose declined markedly beginning in the late 1990s, and by 2012 were at very low levels district-wide while deer numbers remained high. Despite the moose decline being coincident with a short-lived winter tick (*Dermacentor albipictus*) epizootic in the early 2000s and increasing numbers of wolves (*Canis lupus*), we argue that the meningeal worm (*Parelaphostrongylus tenuis*) likely played a major role in this moose decline.

Several factors constrained white-tailed deer (*Odocoileus virginianus*) densities and distribution in the mixed-forest ecotone and regions of the eastern boreal forest until about 200 years ago (Seton 1909, Voigt et al. 2000). Expansion was made possible by forest rejuvenation resulting from human settlement and attendant land clearing, logging, and agricultural practices, as well as increased frequency of forest fires (McShea et al. 1997). As well, Mech et al. (1971) documented how widespread reduction or eradication of predators, primarily wolves (*Canis lupus*), aided and abetted the expansion of deer northward. Karns (1980) also argued that the density of deer in northern mixed forests was constrained mostly by the high frequency of cold, deep-snow winters rather than food limitations. Notwithstanding a lack of agreement on the relative importance of these limiting factors, periodic increases in the abundance of deer in the northern forests of eastern North America have had consequences for caribou (*Rangifer*

tarandus) (Racey and Armstrong 2000) and moose (*Alces alces*) (Anderson 1972, Lankester and Samuel 2007).

In the past century, deer at the northern limits of their range in Ontario have reached sustained high densities at least twice; in the 1940s and 1950s and again in the 1990s and 2000s (Thompson 2000b). Moose declined noticeably in the Kenora District in northwestern Ontario (KD) in each of these deer growth periods. These events in Ontario mirrored recent prominent deer eruptions concurrent with pronounced moose declines in the eastern forests of mainland Nova Scotia, the northern mixed forests of Minnesota, and in adjacent northeastern North Dakota (Parker 2003, Beazley et al. 2006, Murray et al. 2006, Maskey 2008, Lankester 2010, Lenarz et al. 2010). Although not universally accepted (Lenarz 2009), the concurrence of sustained high deer populations and falling moose numbers is supported by numerous anecdotal accounts (early authors reviewed by Anderson 1972, Lankester and Samuel 2007) and by empirical data (Whitlaw and Lankester 1994a, b, Maskey 2008).

Within the present day boundaries of the KD, changes in the presence and abundance of a variety of cervids have been particularly dynamic. This area includes the Aulneau Peninsula where, beginning in about 1997, moose declined from more than 1/km² to almost none in <15 years. We review long-term records from KD to better understand the importance of landscape-level forest disturbances, climate, predators, and pathogens including the meningeal worm (*Parelaphostrongylus tenuis*) in determining historical trends in deer and moose populations.

STUDY AREA

The KD of the Ontario Ministry of Natural Resources and Forestry (MNRF,

formerly the Ontario Ministry of Natural Resources) is located in northwestern Ontario (Fig. 1) and is bounded by the province of Manitoba to the west and the Ontario Districts of Red Lake, Dryden, and Fort Frances to the north, east, and south, respectively. The size of the KD changed minimally in 1961, was reduced in total area from 31,530² to 14,189 km² in 1972, and was increased to 19,744 km² in 1992. Administratively, the KD consists largely of 3 Wildlife Management Units (WMUs 6, 7A, and 7B; Fig. 1).

WMU 6 is the most northerly covering ~4,700 km² and has had recent and extensive forestry activity, wildfires, and blowdowns (MNRF unpublished). WMU 7A, the Aulneau Peninsula, is about 832 km² and located south of the city of Kenora in the middle of Lake of the Woods. It has a recent history of limited forest management and infrequent wildfire, and contains no all-weather roads. WMU 7B lies immediately south of WMU 6 and is >9,000 km² with limited agricultural activity near Kenora and a recent history of extensive forest management and wildfire. Moose aquatic feeding areas are abundant among numerous lakes, rivers, and beaver ponds in all 3 WMUs.

The forest of the more southerly portion of KD is representative of the Great Lakes – St. Lawrence Forest Region and the more northerly part is classified as mixed-wood boreal forest (Rowe 1972). The surficial geology is an area of bedrock with little to no topsoil because of repeated glaciation (Zoltai 1961). Rich, glacial-lacustrine deposits of varved clays occur, particularly in low-lying valleys. Hills are often rugged but most rise less than a few hundred meters from valley floors. The climate is characteristically continental, with a slight moderating effect from the Great Lakes marine climate (OMNR 1974); temperatures range
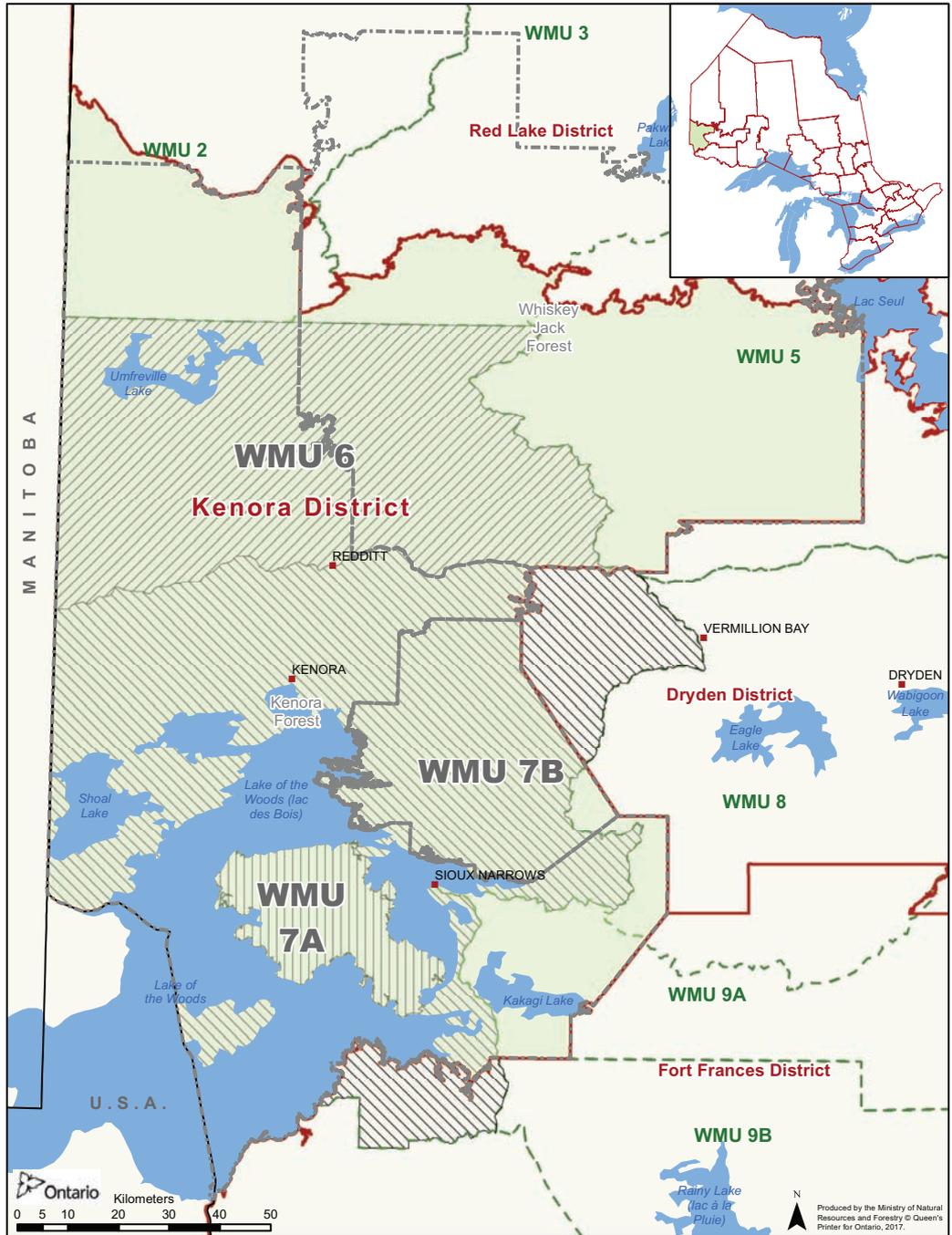
Fig. 1. The Kenora District including its 3 wildlife management units (WMUs 6, 7A, 7B) in northwestern Ontario, Canada.

from a January mean of -17 °C to a July mean maximum of 24.5 °C.

METHODS

The term KD refers hereafter to the actual geographical extent of the MNRF KD and applies collectively to WMUs 6, 7A, and 7B, and as appropriate, to 2 forest management units (MU), the Kenora MU and the Whiskey Jack MU. The boundary of the 2 MUs combined is not identical to that of the MNRF KD; some area extends outside, but in total, the combined area is roughly equivalent in area (Fig. 1).

Landscape-scale disturbance events prior to European settlement and pre-industrial forest conditions are described in broad terms from available internal historical reports and from survey notes on forest cover recorded *circa* 1880 to 1930 (see Elkie et al. 2009). More recent impacts including spatial and temporal aspects of fires, blowdowns, insect damage, and logging are reported at the District level and supported by empirical data from MNRF files. Fire data for the period 1920 to 2010 were reviewed and expressed as numbers of ha burned annually from 1963 to 2007. Large fires (>4000 ha) occurring from 1975 to 2010 were mapped, as were large blowdowns occurring since 1980. Insect infestation data was mostly limited to outbreaks of the eastern spruce budworm (*Choristoneura fumiferana*) and the jack pine budworm (*C. pinus pinus*).

An index of winter severity has been measured in the KD since 1952. Early data (Passmore 1953) were converted to a cumulative, over-winter, snow depth index (SDI) (Warren et al. 1998). Two snow stations have existed in the KD since the onset of the program; a third was added in 1960. One was in WMU 6 near the town of Minaki (MK); the other 2 were in WMU 7B near the towns of

Kenora (KR) and Sioux Narrows (SK). Snow stations were located in open hardwood stands and snow depth (cm) was measured at 10 sites, 10 m apart, and averaged weekly. The weekly averages were summed from the first to last snow of the season. Winter severity was equated to SDI values using the following classification: <590 = mild; 591 to 760 = moderate; >760 = severe (OMNR 1997, Warren et al. 1998, and with permission of MNRF SNOW Network for Ontario Wildlife). The SDI values from each station were averaged to provide a district-wide SDI ranking. Mean differences between time periods for total rainfall, snow depth index, and length of growing season were examined using Student's *t*-test (two-sample, unequal variance) and accepted as different when $P < 0.05$.

Historical weather data including total annual rainfall and the length of the frost-free season were obtained for the KR in the period 1960 to 2013 from the Environment Canada website (http://climate.weather. gc.ca/historical_data/search_historic_ data_e.html). The length of the frost-free season was determined as the difference between the first day of the first 5 consecutive days in spring with minimum temperature > 0 ºC and the day before the first 5 consecutive days in autumn with minimum temperature < 0 ºC.

Several data sources were used to estimate past trends in deer populations, with other information subjective in nature and formed by expert opinion. Data included hunter numbers and deer harvest information collected at check stations and from voluntary questionnaires. District-wide data from 1955 to 1960 were limited to % hunter success, with total deer harvest and % hunter success available thereafter. Two time periods were compared using information pertaining to the KD: 1961 to 1978 and 1999 to 2012. In the intervening time period, 1981 to

1997, only data from WMU 7B were examined in detail. During the time period of 1963 to 1982, pellet group surveys in certain years provided additional deer density estimates in specific wintering areas and the larger landscape. Pellet group surveys in WMUs 6 and 7 from 1976 to 1978 followed King (undated), and a 1982 survey in WMUs 7A and 7B followed Jones (1981). The number of deer observed during moose aerial inventories (MAI) in the KD were recorded as the average number of deer per plot in 2 periods: 1994 to 1999 and 2000 to 2012.

Since 1957, moose numbers and population trends in Ontario (including the KD) have been estimated from mid-winter MAIs based largely on Caughley (1977a, b). After 1972, MAIs were done at the WMU level and their frequency declined after 1992. MAIs were conducted using 16 mi^2 plots until 1975 when standardized surveys for WMUs were adopted using 25 km^2 plots (McLaren 2006). Surveys were random or random-stratified depending on a variety of factors, particularly prior knowledge of relative moose abundance and distribution patterns. They were conducted using both fixed-wing and rotary aircraft, and searches followed the methodology outlined by Oswald (1997). Generally, MAIs in WMUs 6 and 7B were flown with the objective of achieving a 90% confidence level (± 20%). However, MAIs in WMU 7A were often done with 50% coverage which tended to provide higher confidence levels. Voluntary Provincial hunter questionnaires and mail surveys were also used as a proxy to provide estimates of moose populations and to aid moose management.

Black bear (*Ursus americana*) harvests from 1987 to 2010 in WMU 7B were estimated using returns from voluntary Provincial mail surveys (resident hunters) and information from the returns of mandatory Validation Certificates (non-resident hunters). Wolf (*Canis lupus*) sightings in WMU 7B were estimated in 2000 to 2010 using information from Provincial mail surveys sent to resident and non-resident deer hunters.

Office files and the published literature were searched for evidence of the presence of meningeal worm in deer and moose, as well as cases of moose sickness attributed to meningeal worm infection in the KD and surrounding region. Anecdotal information on the occurrence of giant liver fluke (*Fascioloides magna*) and winter tick (*Dermacentor albipictus*) were recorded.

RESULTS

Logging and land clearing — The pre-industrial forest of Ecoregion 4S that includes the KD is believed to have been rich in conifer species (Elkie et al. 2009). Compared to present-day forests, there were more pure stands but similar amounts of young disturbed forest. In general, the pre-industrial forests were believed to have been less fragmented with larger disturbance patches from larger fires. About 20% of Ecoregion 4S is believed to have been in the mixed-wood condition (coniferous and deciduous trees), and only about 1% of the forested area was comprised of pure balsam fir (*Abies balsamae*) stands; presently, ~55% of the forested area is mixed-wood of which 7% is pure balsam fir (Elkie et al. 2009).

Recently approved forest management plans for the Whiskey Jack and Kenora MUs document that logging began in the KD sometime in the early 1800s and has been more or less continuous since the 1880s. Initially, most harvesting was from the nearshore areas of Lake of the Woods and other large lakes in the vicinity, with the harvest rate increasing substantially after 1890. A paper mill was built in Kenora in 1922 further increasing the area logged annually, and a large timberstrand plant opened in 2002.

Table 1. Area of forest harvest (ha), 1990-2014, in the Kenora District Forests, Ontario, Canada.

Decade	Kenora MU	Whiskey Jack MU	Total
1990	10,040	57,584	67,624
2000	13,263	32,425	45,688
2010 (4 years, 40% of decade)	5797	2368	8165

Table 2. Area of landscape-scale disturbances (ha) in the Kenora District, Ontario, Canada.

Fire		Blowdowns		Spruce budworm (1980-98)	
Year	Area (ha)	Year	Area (ha)	Defoliation	Area (ha)
1920s	108,942	1991	50,935	Moderate to severe	26,175
1930s	77,028	2005	67,942		
1940s	8,373			High tree mortality	2,301,341
1950s	1,758				

Although the paper mill in the city of Kenora closed in 2005, a number of local sawmills continue to operate. The area logged annually has varied, but generally, a few 1000 ha of forest are cut annually (< 1% of the total area of KD). Harvest data for the Kenora and Whiskey Jack MUs were available starting in 1990 (Table 1), and MNRF forestry staff report that the greatest amount of harvesting occurred during the 1990s. Clearings associated with early European settlement created an area of a few 1000 ha of field and pasture near the present city of Kenora.

Clearcut logging, the silvicultural practice most commonly used in the KD, produces an abundance of summer forage, although the interior of very large clearcuts (e.g., cover-to-cover distance >400 m) may be used little by deer (Thomas et al. 1979, Roseberry and Woolf 1998) or moose (Hamilton et al. 1980, Thompson and Vukelich 1981, Allen et al. 1987). However, owing to terrain and other factors, clearcuts in the KD have tended to be relatively small.

Fire — The amount of area burned each year in the KD has varied from <100 to >100,000 ha. Large areas burned in the 1920s and 1930s, with fires much less frequent in the 1940s and 1950s (Table 2). More recently, in the mid-1970s to the late 1980s, large areas were again burned, mainly by big fires in 1976, 1980, 1983, and 1988 (Fig. 2 and 3). The area burned annually from 1989 to 2007 was relatively small (generally < 100 ha/year) and has remained so; of note is the absence of fires since 1933 on the Aulneau Peninsula (WMU 7A).

Blow-down — In some years, blow-down affects large swaths of living forest in the KD; forestry staff report that, in general, small blowdown events occur annually. A large blowdown in 1991 covered > 63,600 ha, much of it in WMU 6, and a number of blowdown events in 2005 totaled ~93,000 ha (Table 2, Fig. 4).

Insect damage — Landscape-scale insect damage is attributed to spruce budworm, jack pine budworm, and forest tent caterpillar (*Malacosoma disstria*). Two infestations of spruce budworm in the past century caused substantial mortality of balsam fir, and to a lesser extent, white spruce (*Picea glauca*). Jack pine budworm outbreaks tend to be smaller and infrequent, although a large outbreak resulted in extensive mortality of jack pine in certain areas in 2007-2008. Forest tent
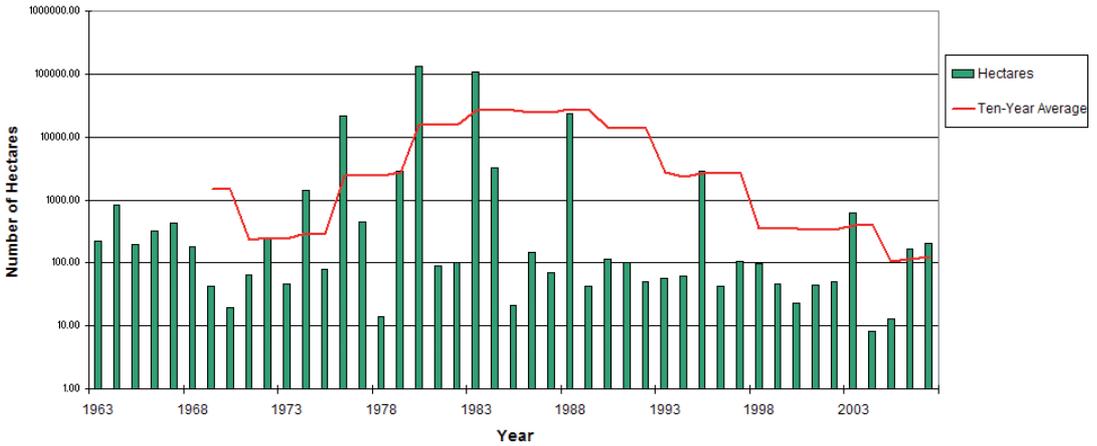
Fig. 2. Number of hectares burned from 1963 to 2007, Kenora District, Ontario, Canada.
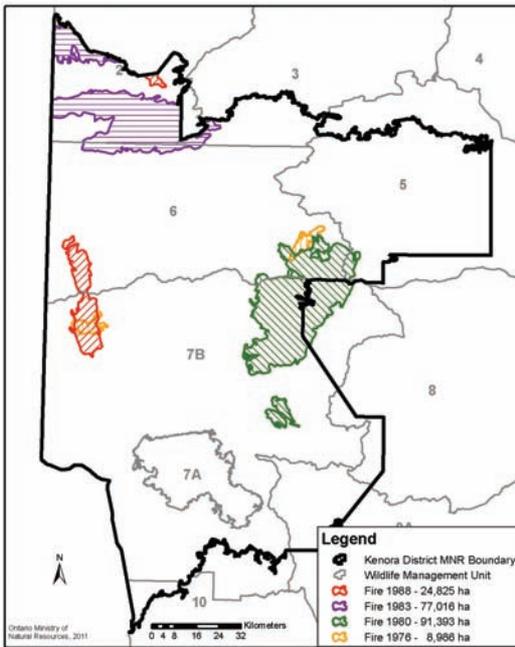
Fig. 3. Forest fires >4,000 ha from 1975 to 2010, Kenora District, Ontario, Canada.
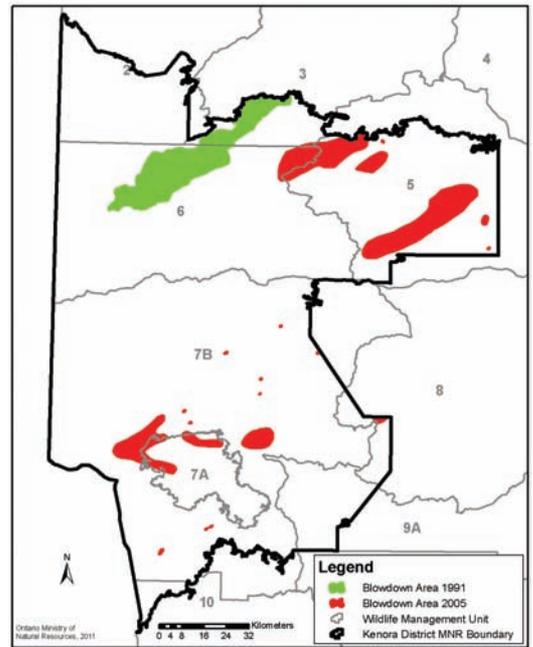
Fig. 4. Large blow-downs in forests from 1980 to 2010, Kenora District, Ontario, Canada.

caterpillar outbreaks are cyclical (~10 years), but they prefer aspen (*Populus* spp.) and trees tend to recover quickly from defoliation.

In 1934, a spruce budworm outbreak reached 'epidemic proportions' and by the end of the outbreak in 1947, 5.3 million ha of Ontario had been infested, including a sizeable portion of the KD. The second spruce budworm epidemic occurred from about 1980 to 1998, with >8.3 million ha of Ontario forests infested. Substantial tracts of forest in the KD were categorized as having "moderate to severe defoliation" and >2 million ha had "high tree mortality" (Table 2, Fig. 5).
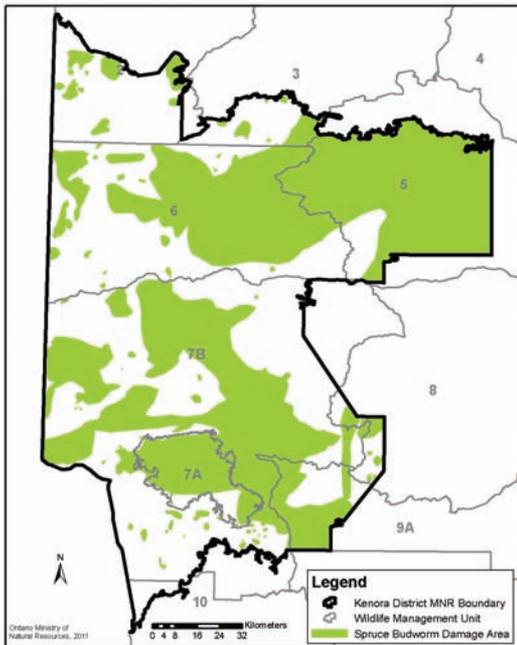
Fig. 5. Forests with significant spruce budworm damage in 1998, Kenora District, Ontario, Canada.

Before the second spruce budworm infestation, Kenora OMNR management staff estimated that balsam fir composition was ≥ 40% in mixed-wood forests. In the later stage of the epidemic, tree lichen (*Usnea* spp.), was very abundant where balsam fir mortality was high (Fig. 5). Its availability peaked in the early 2000s, but by 2010, one author (Ranta) observed that most dead balsams once laden with lichens had fallen, and most lichens had been (presumably) consumed.

The Aulneau Peninsula — Of particular note is WMU 7A, the Aulneau Peninsula which had no large fires or blowdown since 1933 (OMNR 2003), although the effects from spruce budworm were widespread (Fig. 5). Beginning in 1964, however, ~15,000 m³ were logged annually, generally as small (<100 ha) dispersed cuts that District staff believe greatly improved moose habitat conditions; logging ceased in 1986 and has not resumed. A substantial

portion of the Aulneau and some parts of WMU 7B had a pronounced loss of coniferous canopy cover as a result of the jack pine budworm outbreak in 2007-2008. Although these infestations result in minimal growth of arboreal lichen on dead and dying jack pine trees, removal of the over-story likely stimulated growth in the understory.

Winter snow depth — Winter severity rankings for the 3 snow stations (SN, KR, and MK) ranged from very mild to severe (Fig. 6). Mean (± SD) annual SDIs were greater ($P = 0.03$) in the period from 1960 to 1980 (801 ± 231) than in the subsequent period from 1981 to 2014 (632 ± 241). The most southerly station (SN) had lower ($P = 0.03$) mean SDI in the period from 1960 to 2014 (616 ± 235) than the two more northerly stations that were similar (KR = 732 ± 266; MK = 719 ± 244). Severe winters with an SDI > 760 were most frequent in the 20-year period from 1960 to 1980 when 11 winters were rated as severe and only 3 as mild (<590); over the next 34 years (1981 to 2014) only 7 winters were rated as severe with 16 as mild (Fig. 6).

The average maximum snow depths from 1952 to 2014 at the 3 snow stations were 55.4 cm (KR), 54.8 cm (MK), and 50.8 cm (SN). Weekly readings exceeded 80 cm on only a few occasions and those depths were generally of short duration; depths >90 cm were recorded in only 2 winters (1955-56 and 2013-14). In the MK depths >80 cm were recorded for 3 consecutive weeks in 1954-55, and for 7 consecutive weeks the following year. In the winter of 1965-66, all 3 snow stations had 1 weekly recording >80 cm; a single weekly reading was 81 cm at KR in 1977-78. During the recent severe winter of 2013-14, snow depth >80 cm occurred at both KR and MK; the maximum depth was 72 cm at SN.

Annual rainfall and length of the frost-free season — The amount of rainfall and
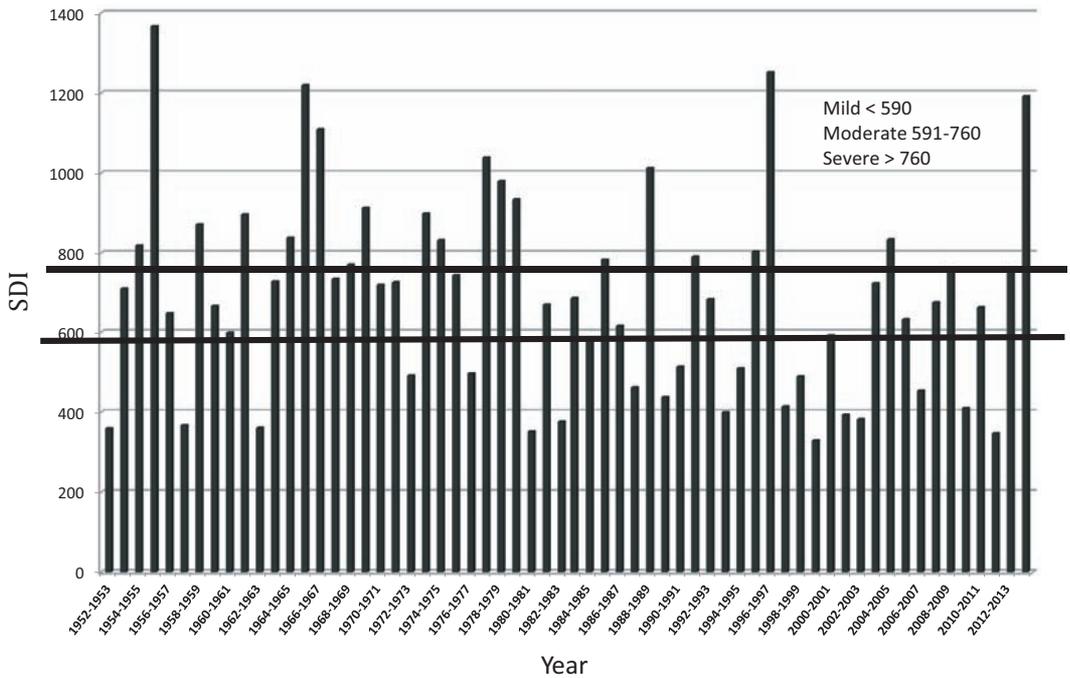
Fig. 6. Snow depth index (SDI) averaged for 3 snow stations (Sioux Narrows, Kenora, and Minaki) from 1952 to 2014, Kenora District, Ontario, Canada.

the length of the frost-free season are climatically important in the external survival and transmission of parasites such as *D. albipictus* and *P. tenuis*. The 20-year period from 1970 to 1990 that had several large fires also received less ($P = 0.01$) rain (474 ± 115 mm) than in the following 20-year period from 1991 to 2012 (609 ± 120 mm). The mean length of the frost-free period between these time periods was not different (185 ± 16 vs. 188 ± 18 days), ranging from 156 to 214 days and 156 to 223 days, respectively.

Historical cervid populations — In the late 1800s, caribou and moose occurred in what is presently KD (Cumming 1972, Darby et al. 1989). Seton (1909) believed that deer were largely absent until the late 1800s, but some elk (*Cervus elaphus*) were extant. Caribou range began to recede northwards concurrent with the increase in deer numbers (Racey and Armstrong 2000), with elk disappearing also; moose remain extant to the present.

Trends in deer numbers — By the 1930s, deer were numerous in the KD and stayed high during the 1950s and early 1960s (Cumming 1972). By the late 1960s, deer numbers began to decline, increased somewhat, again declined, then remained relatively low until the mid-1980s (Fig. 7). Thereafter, deer numbers steadily increased, peaking about 2007. In 2014 a severe winter resulted in high deer mortality and likely substantial recruitment failure. Declining hunter success and field observations suggested that deer in the northern portions of KD and deer away from settlements were most affected.

Records of the number of hunters and deer harvest for WMUs 6, 7A, and 7B showed a similar trend from 1974 to 2012 (Fig. 8). The annual deer harvest fluctuated, but was relatively low through the 1970s. By the late 1990s, hunter interest and success rates had begun to increase and remained
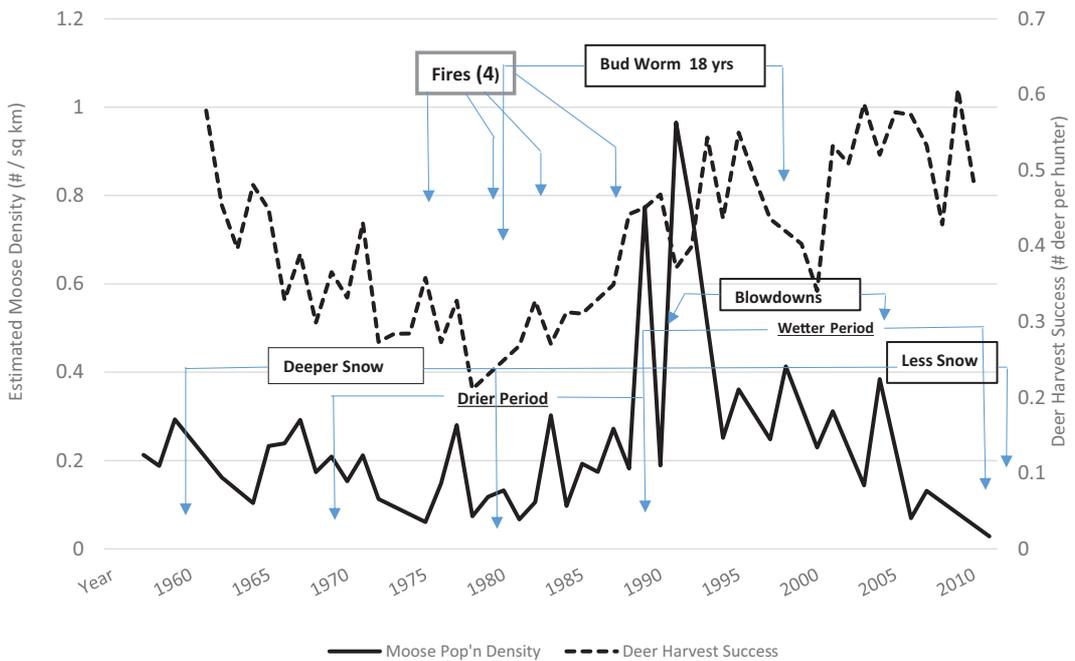
Fig. 7. Changes in deer and moose numbers in relation to landscape scale habitat disturbances from 1955 to 2014, Kenora District, Ontario, Canada.
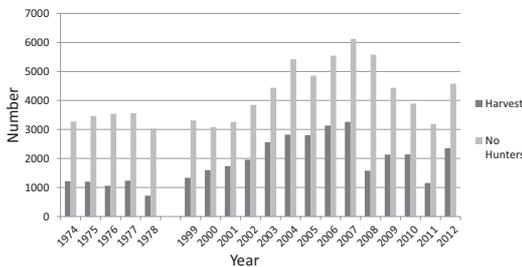
Fig. 8. Deer hunters and harvest for WMUs 6, 7A, and 7B, 1974 to 2012, in the Kenora District, Ontario, Canada.
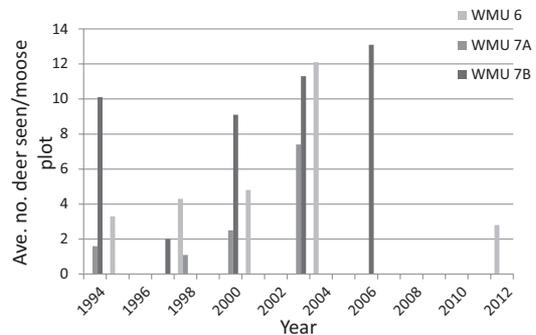
Fig. 9. Number of deer observed per moose aerial survey plot in WMUs 7A, 7B, and 6, Kenora District, Ontario, Canada.

high except in 2008 and 2011. In 2002, deer hunting regulations were relaxed and hunters could purchase additional antlerless deer tags in WMUs 6, 7A, and 7B. Data from this additional deer kill is only available starting in 2008, hence, total deer kill in 2002-2007 is under reported. The number of deer observed per moose plot clearly increased in each of the 3 WMUs by the late 1990s, continuing through 2006 (Fig. 9).

Spring pellet group surveys provided a few disjunct estimates of winter deer populations in portions of WMU 7 in 1976 and 1977, and the entire WMU 6 in 1978 (Ranta and Shaw 1982). Density estimates were: WMU 7 - 1976, $4/km^2$ (14,557 ± 54.4%); WMU 7 - 1977, $4/km^2$ (15,515 ± 28.9%); WMU 6 - 1978, $1/km^2$ (3,362 ± 36.93%). Recalculation of the WMU 7 - 1977 survey

data led to a higher estimate of 31,000 deer. In 1979, in response to a suspected drastic population decline after a severe winter, supplementary pellet group surveys were performed and indicated that the deer population in WMU 6 had declined 75% from the previous year, and in WMU 7, 55% from 2 years previous. The mid-winter deer population estimate from pellet group surveys in 1982 was only $47 \pm 76.8\%$ in WMU 7A and $10,231 \pm 41.2\%$ in WMU 7B (Ranta and Shaw 1982). Deer numbers were considered relatively low throughout the period of 1976 to 1982.

Trends in moose numbers — Moose were described as fairly common in the Lake of the Woods area by Europeans as early as 1731 (Cumming 1972, Darby et al. 1989). The population declined in the 1800s with the growing population of settlers, survey crews, and road builders relying largely on market meat. In response to perceived low populations, the moose hunting season was closed across the entire province from 1888 to 1895; thereafter, moose numbers apparently increased.

There are few estimates of moose numbers in the KD in the early years of the 20th century. Cumming (1972) reported that the Royal Ontario Museum (from questionnaires) believed that the provincial moose population declined prior to WWII, increased during the war years, but was considered low in 1949 when the hunting season was again closed. It was re-opened in 1951 when populations across the province appeared to have increased, although actual population estimates only began in the late 1950s.

In 1957, MAI data indicated that moose were at fairly constant and moderate density of ~0.2/km^2 (Fig. 7). As deer numbers declined in the 1960s, moose numbers increased slowly, continuing into the late 1980s and 1990s when they peaked ~ 0.4/km^2; beginning about 1995, moose began to decline reaching
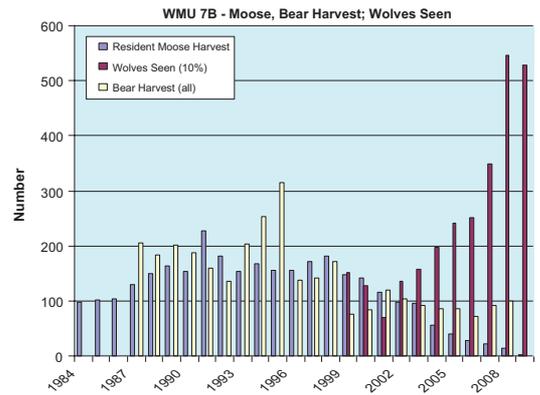
Fig. 10. Hunter harvest of moose and bear, and number of wolves observed by hunters in WMU 7B, 1984-2010, Kenora District, Ontario, Canada.

very low numbers by 2012 (Fig. 7). Moose hunter survey information in WMU 7B (Fig. 10) was used to corroborate the MAI data. Increased harvest began in the late 1980s until about 2001, after which success rates began to decline to present day lows. Concurrently, deer numbers increased until about 2007, remaining high to 2012 (Fig. 8). After the severe winter of 2014, deer numbers declined throughout the KD and adjacent Districts (unpublished MNRF data).

When the MAI data for the 3 WMUs are examined separately for the years 1980 to 2010, it appears that the timing of the moose decline differed slightly in each (Fig. 11). A decline from high density was first evident in the most southerly unit (WMU 7A) after 1995, a distinct decline occurred in WMU 7B after 2001, and decline occurred after 2004 in the most northerly WMU 6; numbers remain low in all. In 1972 on the Aulneau peninsula (WMU 7A), the moose population was estimated at only ~80 animals (about 0.1/km^2), but by 1994 had peaked at ~1000 animals (about 1.0/km^2) with numbers still relatively high in 2000; however, rapid decline occurred thereafter, and an aerial survey estimated only ~30 animals in 2011 (< 0.04/km^2).
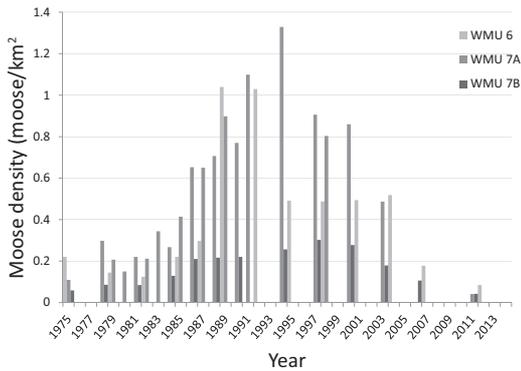
Fig. 11. Moose estimated from aerial inventory in WMUs 6, 7A, and 7B in 1975 to 2012, Kenora District, Ontario, Canada.

Predators — Both black bears and timber wolves are common and ubiquitous in all 3 WMUs. Data from early years are largely limited to anecdotal information, but no concerns about either animal being 'rare' or in decline are on record. Bear harvest from 1988 to 2009 rapidly increased, peaking around 1996 in all WMUs (Fig. 10). Thereafter, harvest declined sharply with the lowest combined harvests in 2006 and 2007 across the WMUs; harvest declined least on the Aulneau (WMU 7A) and most in WMU 7B. Records of wolf sightings by deer hunters in WMU 7B began in 2000 and indicated an initial wolf decline for 3 years, followed by a large increase to 2010 (Fig. 10).

Evidence of meningeal worm and other pathogens — A number of surveys have documented the continued presence of *P. tenuis* larvae in deer feces and moose deaths attributed to meningeal worm in northwestern Ontario and adjoining regions. The prevalence of first-stage larvae in deer pellets ranged from 57-85% in the KD (Saunders 1973, Whitlaw and Lankester 1994b, McIntosh 2003) and 86% in the adjacent Fort Frances District (McIntosh 2003). Also in the Fort Frances District, 3 cases of moose sickness caused by *P. tenuis* were diagnosed by Anderson (1965) and 14 cases

were reported to the District Office during the 12-year period 1980 to 1992 (Whitlaw and Lankester 1994b). In the early 2000s, one of the authors (Ranta) examined a number of sick, dying, and dead moose from WMUs 6 and 7B that displayed classical symptoms of meningeal worm infection. The disease has been documented in adjacent southeastern Manitoba where Lankester (1974) recorded 13 cases within a 12-month period in 1972-73.

Giant American liver fluke (*Fascioloides magna*) is known to occur in deer of the KD but no data exist about its relative abundance. We know of no reports from hunters of noticeably infected moose for at least the last 3 decades. Winter ticks are regularly seen on moose in early spring, and reports from outfitters, trappers, and moose hunters suggest that a substantial die-off of moose occurred in WMUs 7A and 7B in 2000 and 2001 when moose density was high (Fig. 7 and 11). Anecdotal evidence on the Aulneau Peninsula included a number of moose skeletons located the following spring, summer, and fall.

DISCUSSION

Data presented here indicate that deer and moose populations in KD have experienced significant population swings over the past 100 years, and disturbances at the landscape scale have impacted both species. Logging and land clearing are likely responsible for the initial invasion and subsequent maintenance of deer in the District, despite periodic die-offs associated with severe winters. Both logging and fire are also believed responsible for an increase in moose in British Columbia and northern Ontario (Thompson and Stewart 1998). In Ontario, relatively high moose populations are typically found in forested areas with a mosaic of vegetation types providing a high interspersion of cover and forage (Rempel et al. 1997).

Formalized moose habitat guidelines used in Ontario and the KD since 1988 provide a detailed summary of the benefits of good forest management practices (OMNR 2010).

Logging, combined with forest fire suppression, leads to shifts in forest composition and structure (Carleton 2000). Balsam fir is one species that becomes more prominent in managed forests (Thompson 2000a), making the forest more susceptible to spruce budworm infestation and blowdown. Infestations cause stand mortality after 5 consecutive years of defoliation (Fleming et al. 2002) followed by peeling bark, growth of draped arboreal lichen (*Usnea* spp.), and top breakage culminating in wind-throw 5 to 8 years later. Peaks of deer abundance in the mid-1900s and early 2000s appear to be strongly associated with fir mortality and associated abundance of lichen. While balsam fir is generally not considered preferred deer browse (e.g., Ullrey et al. 1968, Mautz et al. 1976), the arboreal lichen associated with dead and dying balsams is heavily used by deer during winter (Hodgman and Bowyer 1985). *Usnea* spp. compares favourably with respect to crude protein, available energy, and relatively high digestibility of typical hardwood winter browse (Hodgman and Bowyer 1985, Gray and Servello 1995).

No evidence of impacts to deer or moose were evident from forest tent caterpillar outbreaks, although both species would presumably have access to improved quality and quantity of understory forage in the immediate aftermath of an outbreak. Similarly, the effects of the jack pine budworm and associated loss of coniferous canopy should seasonally benefit both deer and moose.

The last peak in the KD moose population is attributed primarily to the large fire events of the 1980s; considerably less area has burned since. MAI found high concentrations of animals in and immediately adjacent to the large burns of the 1980s, but more recent surveys indicate few moose in these same areas. The association of moose with early seral stages of post-fire habitat has long been recognized (Peek 1997). Kelsall et al. (1977) concluded that the optimal successional stage for moose in the boreal forest occurred 11 to 30 years post-burn, and moose in Alaska respond positively to fires as early as 5 years post-burn (Schwartz and Franzmann 1989). Although deer have an abundance of food in the early aftermath of fire, the loss of conifer cover in winter yarding areas can seriously jeopardize winter survival (Hanley and Rose 1987, Broadfoot and Voigt 1996). Fires can eliminate balsam fir from stands (Thompson 2000a), and little balsam fir was left in the KD burns. Because these large burned areas lacked winter conifer cover and associated lichen as winter forage (*Usnea* spp. do not thrive on fire-killed balsam fir), these burns presumably become unsuitable for deer in deep snow.

A severe winter can dramatically lower deer density on northern ranges and limit range occupancy (Potvin et al. 1981). High mortality can occur when deep snows of long duration are coupled with extreme cold (Severinghaus 1947, Verme 1968, Verme and Ozoga 1971), conditions that affect fawns in particular (Karns 1980). The combination of severe winter conditions and predation by wolves produces higher deer mortality than either factor acting alone (Mech et al. 1971).

Winter severity indices are helpful to identify winters when substantial deer losses likely occur, but the typical values measured most years in the KD are not believed high enough to negatively impact moose. Peek (1997) found moose tolerant of snow depths up to 80 cm, and Coady (1974) identified 90 cm as a critical depth when adults have restricted movement and access to forage.

Winters with snow depths >90 cm are rare in the KD, but depths of >40 cm that restrict deer movement occur regularly (Kelsall and Prescott 1971). Weekly SDI values indicate that snow depths >75 cm occur occasionally. At these depths, deer are in a severe energy deficit due to restricted and energy-costly movement, even when browse is abundant (Potvin and Huot 1983).

Both moose and deer populations in the KD increased during the 1980s and 1990s in response to increased forage created by a variety of large landscape scale disturbances, and low snow depths that specifically favour deer survival. Moose experienced a pronounced decline beginning about 1995, reaching very low levels by 2012 as deer numbers remained high. Similar moose declines occurred concurrently in eastern North America and in jurisdictions neighbouring the KD. For example, populations began to decline in the early 1990s and were reduced to low numbers by 2003 in Nova Scotia (Beazley et al. 2006), moose declined in the late 1980s with few occurring by the early 2000s in northwestern Minnesota (Murray et al. 2006), and numbers peaked about 1995 but moose had virtually disappeared in northeastern North Dakota by 2006 (Maskey 2008). A similar increase in deer and decline in moose also occurred in southeastern Manitoba during this time frame (V. Crichton, Manitoba Fish and Wildlife, retired, pers. comm.). These declines followed periods of shorter, less severe winters that sustained high density populations of deer with meningeal worm (Lankester 2018); longer and wetter growing seasons were also associated with some of these declines (Maskey et al. 2015). Typically, declines continued for 15-20 years reaching very low levels that persist to the present. It has been argued that the meningeal worm was a principal cause of these declines (Maskey 2008, Lankester 2010,

2018), and our observations parallel those in other regions.

Moose with winter tick-associated hair loss were commonly observed during MAI surveys in the Kenora MU and unusually high over-winter mortality was reported following the winters of 2000 and 2001 when moose densities were still relatively high. Carcasses and skeletal remains found in a fashion inconsistent with mortality from predation were likely due to disease or parasitism, but the exact cause of these winter mortalities was never identified. Winter tick numbers are not influenced by the presence or absence of deer and they have their greatest impact when moose densities are high. These ticks typically cause late winter mortality for a few successive years and then subside in abundance at lower moose density or environmental conditions that reduce larval survival and/or the questing period. Winter ticks alone are not thought to be capable of driving moose populations to low levels in a short time frame (Lankester 2010).

The giant liver fluke is not prominent in the KD and cannot be considered a major contributor to the moose decline, as this parasite has not been proven to cause large-scale moose mortality. Heavy fluke infections were interpreted as being significant in a declining moose population in northeastern Minnesota (Murray et al. 2006), yet flukes were equally common when that same moose population was increasing 20 years earlier (Karns 1972, Lankester 2010). Flukes were not considered important in the moose decline in adjacent northeastern North Dakota (Maskey 2011) and do not occur in Nova Scotia (Pybus 2001) where pronounced moose declines have occurred twice.

Records of wolf sightings by deer hunters became increasingly common in the KD from about 2000 to 2012, the same period in

which deer reached peak numbers and moose declined to low levels. This was also the period in which the effects of meningeal worm on moose were expected to be greatest making it difficult to separate the relative roles of parasites and wolves in the decline. Classically, wolves increase in response to increased deer numbers and may depress productivity of co-habiting moose by preying disproportionately on calves. Wolves are also likely to find moose handicapped by *P. tenuis* infection particularly easy prey. Yet, in most instances, wolves are not expected to reduce their prey to extremely low levels (Mech 1970, Mech and Karns 1977). As well, several studies have shown that where deer and moose co-exist, wolves tend to concentrate on deer whether deer numbers are increasing or declining (Pimlott et al. 1969, Mech et al 1971, Potvin et al. 1988).

A prominent role for wolves in declines elsewhere is even less likely as wolves do not occur in mainland Nova Scotia, and the resident eastern coyote (*Canis latrans*) is not considered a significant predator of moose (Parker 2003) or to have played a substantial role in mainland Nova Scotia moose being declared "endangered" after the recent decline. Nor were wolves considered a main factor in moose declines in northwestern (Lenarz et al. 2009) or northeastern Minnesota (Murray et al. 2006), or in neighbouring northeastern North Dakota (Maskey 2008). However, Mech and Fieberg (2014) argued for caution in accepting the conclusion of Lenarz et al. (2009) that elevated winter temperatures caused the impending decline of moose populations in northeastern Minnesota, and instead suggested a stronger role for wolves. Current research has identified that *P. tenuis* and wolf predation are principal mortality factors in Minnesota moose (M. Carstensen, Minnesota Department of Natural Resources, pers. comm.).

Hunting can reduce deer and moose numbers and significant declines may result, especially when stricter regulations are not implemented quickly enough in response to natural stochastic population changes (Fryxell et al. 2010). However, there is little evidence that inordinately high hunter harvest (Fig. 10) caused the abrupt and prolonged decline of moose in the KD. Deer invariably decline following severe winters, and hunter harvest played a minimal role in the 1970s decline (Ranta 1982). Further, deer began to increase in the 1980s and continued to increase until about 2007 despite increasing hunting pressure.

Several climatic factors known to enhance transmission of *P. tenuis* circumstantially support a major role for this parasite in the KD moose decline. Shorter winters with less snow and lower SDIs during the 1990s and 2000s allowed increased deer densities, and in particular, increased survival of fawns. Fawns are the biggest producers of the parasite's larval stages and an early spring increases larval survival (Lankester 2018, in press). Also, the length of frost-free seasons during this period increased, albeit marginally, but growing seasons were much wetter than in the previous 20 years. Precipitation is an important driver of terrestrial gastropod populations and determines the extent to which they move on the forest floor to become infected and ingested by cervids (Wasel et al. 2003).

Caribou are much more susceptible than other cervids to neurological disease caused by meningeal worm infection (Anderson 1972). Records of range recession of caribou in northwestern Ontario indicate that caribou disappeared from most of the present day KD during the first era of high deer densities (Darby et al. 1989), and are now found only on the northern fringe of the KD (Ranta 2001).

CONCLUSION

Landscape level factors, working in synergy, have been primary population-level drivers behind widely fluctuating populations of deer and moose in the KD in much of the past century. However, habitat availability, winter conditions, and predation cannot adequately explain the moose decline in the KD. Much evidence suggests that pronounced and prolonged declines in moose populations result when specific conditions occur concurrently: 1) when the distribution of moose and infected (*P. tenuis*) deer are sympatric, 2) when winter conditions are generally favourable for survival, growth, and expansion of deer populations for many consecutive years (e.g., > 10 years), and 3) when environmental conditions are favourable for the survival and mobility of terrestrial gastropods required for transmission of the meningeal worm - as illustrated in Fig. 7. We suggest that the meningeal worm played a major role in the recent moose decline in the KD and is likely to have done so repeatedly in several locations in eastern North America within the past century (Lankester 2018).

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