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Population Ecology

Moose Calf Mortality in Central Ontario, Canada

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ABSTRACT Although some populations remain stable, moose (*Alces alces*) density and distribution have been declining in many areas along the southern edge of their North American distribution. During 2006–2009, we deployed 99 vaginal implant transmitters (VITs) in 86 adult female moose in central Ontario, Canada to assist in locating and radiocollaring neonatal moose calves. We monitored radiocollared calves to estimate calf survival and assess the relative importance of specific causes of death. Calves in the western portion of our study area (WMU49) were exposed to a 6-day general hunting season, whereas calves in the eastern portion of our study area (Algonquin Provincial Park [APP]) were not exposed to hunting. Annual survival for 87 collared calves was greater in the protected area than the harvested area (72.4 ± 6.8% and 55.8 ± 8.3%, respectively) and averaged 63.7 ± 7.1% overall. Predation by wolves (*Canis* sp.) and American black bears (*Ursus americanus*) was the dominant cause of death but occurred predominately in APP, whereas other natural mortality agents were 4× more common in WMU49. Only 16% of the collared calves in WMU49 were harvested each year despite a high proportion (approx. 50%) of accessible, public land. Most natural mortality occurred prior to the autumn hunting season such that reductions in natural mortality had little potential to compensate for calf harvest. Overall, calf survival in our study area was moderate to high and our findings suggest predator control or further restrictions of calf hunting in this area is not justified.

KEY WORDS *Alces alces*, black bear, cause-specific mortality, eastern wolf, hazard, hunting, moose, Ontario, survival analysis, *Ursus americanus*.

Juvenile mammals of many species tend to be more vulnerable to predation than adults (Gaillard et al. 1998, 2000). However, this is often seen as relatively unimportant among ungulates because adult survival typically has a much greater influence on population growth rate (λ; Escos et al. 1994; Walsh et al. 1995; Gaillard et al. 1998, 2000; Eberhardt 2002). Yet, for populations typified by low and variable juvenile survival, variation in juvenile survival can profoundly influence λ (Raithel et al. 2007). Predation on calves is a major limiting factor for many moose (*Alces alces*) populations (Larsen et al. 1989, Testa et al. 2000, Bertram and Vivion 2002), and given the importance of moose as a game species in many areas, this issue has received much attention.

Historically, moose distribution extended through much of the mixed coniferous–deciduous forest of North America, but declined to low levels in the late 1800s because of overharvest and habitat loss (Boer 1992, Alexander 1993, Courtois and Lamontagne 1997). Recent habitat restoration, conservative harvest regulations, and the creation of parks and reserves have enabled recovery of some southern moose populations (e.g., Bontaites and Gustafson 1993, Timmermann and Buss 1997, Musante et al. 2010), whereas others either have not recovered or have continued to decline (e.g., Pulsifer and Nette 1995; Hurd 1999; Murray et al. 2006; Lenarz et al. 2009, 2010).

In response to declining moose populations, the Ontario Ministry of Natural Resources (OMNR) introduced a comprehensive moose management policy in 1980 (OMNR 1980). One outcome of the new policy was implementation

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of a selective harvest program for moose in 1983. Under this program, a limited number of tags for adult moose was offered in each wildlife management unit (WMU), but hunters could legally kill 1 calf moose in any WMU with an open moose season (Euler 1983). This system presumed that hunting mortality of moose calves was largely compensatory relative to other mortality factors (Euler 1983). Although both the harvest and size of the moose population initially increased under this system, broad-scale declines in moose numbers, and in particular estimates of winter calf:cow ratios, caused concern across much of Ontario's moose range during the 1990s and early 2000s (Heydon et al. 1992, Timmermann et al. 2002). In 2002, OMNR reduced the number of adult tags in some WMUs and implemented a lottery system for calf tags (OMNR 2003). Public controversy revealed a split in perception regarding factors responsible for declining calf recruitment and moose numbers; many hunters attributed the declines to predation by wolves (*Canis* sp.) and American black bears (*Ursus americanus*), whereas many biologists considered excessive harvest to be at least partially responsible (OMNR 2003, Brown 2011). In light of these disparate views, our objective was to determine the relative importance of natural versus human-caused mortality of moose calves near the southern edge of their range in central Ontario. Our objective was to determine the degree to which harvest of moose calves was additive to other mortality factors by comparing mortality patterns of moose calves in a protected area with those in a harvested area. Specifically, we predicted that if hunting mortality of moose calves was largely additive then 1) mortality due to predation and other natural causes would be similar between the 2 study populations, and 2) total mortality would differ by an amount similar to the rate of hunting mortality.

STUDY AREA

We studied moose in central Ontario, Canada (45°N, 78°W) within the western region of Algonquin Provincial Park (APP; 2,000 km^2) and the southeastern portion of WMU49 (1,500 km^2; Fig. 1). This study area was near the southern distribution of moose range in Ontario (Murray et al. 2012), and occupied the northern portion of the Great Lakes-St. Lawrence Forest Region near the convergence with the boreal forest (Cook et al. 1999). The 2 study sites were separated by roughly 50 km. Western APP consisted of a protected forest with limited forest harvesting and no moose harvest; WMU49 included public and private lands where logging and moose harvest occurred. Forest cover in APP was dominated by sugar maple (*Acer saccharum*), poplar (*Populus* spp.), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), spruce (*Picea* spp.) and fir (*Abies* spp.); the forest composition in WMU49 was comparable, although

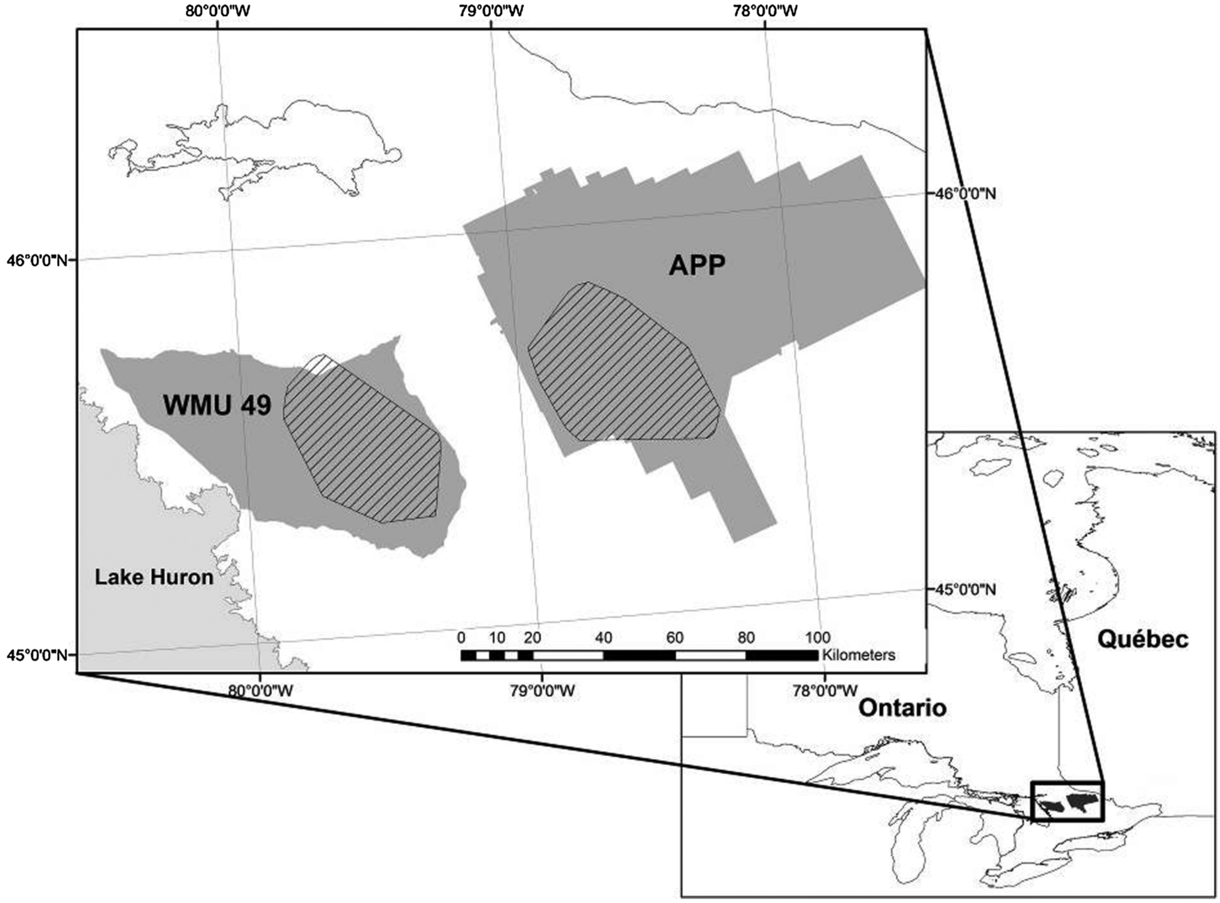

Figure 1. Location of moose calf study areas in Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49) in central Ontario, Canada, 2006–2009. The 2 study areas are hatched.

with less hemlock and more habitat fragmentation due to development and agricultural land (Crins et al. 2008). The study sites differed in elevation, with APP (320–580 m ASL) approximately 200 m higher than WMU49 (73–549 m ASL). Environmental conditions during our study were typical for the area. From 1971 to 2004, the long term normal for daily average temperatures in January and July averaged −11 °C and 18° C, respectively (APP East Gate Station: 45°31.8′N78°16.2′W; Environment Canada 2008). Potential predators of moose in the region included eastern wolves (*Canis lycaon*) and black bears. Wolves were moderately abundant in APP (2.3–3.0/100 km^2; Patterson et al. 2004) but less common in WMU49, where most free-ranging canids were eastern coyotes (*Canis latrans var.*) and wolf–coyote hybrids (Benson et al. 2012). Black bear densities were estimated to be 45 ± 10 km^2 and 31 ± 9/100 km^2 (mean ± SE) for WMU49 and APP, respectively (Obbard et al. 2012). White-tailed deer occurred at intermediate densities in both areas, but were largely absent from APP during winter. Within 50–100 km to the south of the study region, contiguous forest cover became increasingly fragmented and gave way to agricultural lands and increased human land use.

METHODS

Calf Capture and Collar Deployment

Beginning in May 2006 in APP, we surveyed islands and peninsulas with known calving histories with crews of 6–12 people (Addison et al. 1985, Garner 1994). Specifically, we walked parallel transect lines within sight of adjacent crew members. When we encountered cow moose with calves, we attempted to drive them to water and pull the calf into a waiting motorboat. When successful, we blind-folded and processed calves in the boat. When we could not employ this strategy, we captured the calf by hand on land. When we processed calves on land, 2–3 people fit the radiocollar and took measurements while the remainder of the crew kept the cow at bay by hazing. Most dams of calves captured by this method were not radiocollared (Table 1). We estimated parturition dates by backdating from the estimated age of neonates; we estimated calf ages as <1 day, 1 day, 2 days, 3–7 days (5 days), or >7 days based on coordination, mobility, wet or dry appearance, and presence of an umbilicus (Larsen et al. 1989). We ear-tagged, sexed, and weighed calves and fitted each with expandable radiocollars (M4210, Advanced Telemetry Systems, Inc. Isanti, MN; TS30, Telemetry Solutions, Concord, CA). We released calves captured in water at the point at which they entered the water.

The systematic searches of known calving areas described above did not provide random sampling within the study area. In 2007, we began using encapsulated vaginal implant transmitters (VITs; M3970, Advanced Telemetry Systems, Inc.) to locate and capture calves from a random sample of cows in both study areas. From January through March, 2007–2009 a helicopter-borne crew captured 119 different adult (mean age = 4 ± 2 [SD] years; range: 1–9 years old) female moose by darting or aerial net gunning and fitted them with either very high frequency (VHF) or Global Positioning System (GPS) collars (see Lowe et al. 2010, Murray et al. 2012; Lotek 3300L, Lotek Wireless, Inc., Newmarket, ON, Canada; Telemetry Solutions Quantum 5000; 5000b, Telemetry Solutions). In 2007 and 2008, the crew darted moose using a mixture of carfentanil (Wildlife Pharmaceuticals, Inc., Fort Collins, CO) at approximately 0.0070 mg/kg body weight combined with xylazine hydrochloride (Rompun®; Bayer, Inc., Etobicoke, Ontario, Canada) at approximately 0.2 mg/kg body weight. They subsequently reversed this drug combination with naltrexone

Table 1. Number of neonatal moose calves captured opportunistically and by monitoring radiocollared dams fit with vaginal implant transmitters (VITs) in Algonquin provincial park (APP) and Wildlife Management Unit 49 (WMU49) in central Ontario, Canada, 2006–2009.

Study area and year	No. VITs deployed	No. VITs functioning at start of calving season	No. VITs shed in-year	No. VITs recovered <48 hours after parturition	No. successful collaring events involving cows fit with VITs[a,b]	No. successful collaring events involving non-instrumented cows[c]
APP						
2006						12
2007	7	7	5	1	0	15(3)
2008	18	17	16	10	0	4
2009	10	10	9	5	1(1)	8(2)
Total	35	34	30	16	1(1)	39(5)
WMU49						
2007	15	15	13	9	7(1)	0
2008	13	12	10	10	7(1)	0
2009	36	32	27	27	23(2)	0
Total	64	59	50	46	37(4)	0

[a] The number of twinning events is given in parentheses, thus a record of 7 (1) indicates that 8 calves were collared.

[b] We were unable to capture calves belonging to most cows fit with VITs in APP either because of cow aggression or because the cows calved in remote areas and we were unable to visit the birthing sites before the calves became mobile enough to evade capture. Of the 16 cases during which we were unsuccessful in collaring calves of cows fit with VITs in WMU49, 2 cases involved stillborn calves, 3 VITs were shed >24 hours prior to calving, 4 VITs failed during the calving season either before or just after expulsion, and in the remaining 7 cases the calf was either confirmed to be present but too mobile for manual capture ($n = 4$), else no calving bed was found near the VIT recovery site and the dam was never subsequently observed with a calf during that year ($n = 3$).

[c] Although VITs were not involved, calves of 2 radiocollared cows were captured during 2006 and 2007.

at approximately 0.7 mg/kg. In 2009, Pathfinder Helicopters (Salt Lake City, UT) net-gunned all captured cows from a helicopter and manually restrained them without use of chemical immobilization.

We deployed 99 VITs in 86 captured adult females (9 moose were fit with VITs during 2 winters and 2 moose were fit with VITs during 3 consecutive years). We were unable to assess pregnancy prior to deployment of VITs; however, we determined pregnancy status post-capture based on serum progesterone. We assumed that cows with serum progesterone >2.5 ng/ml had been pregnant at time of capture (Murray et al. 2012). Prior to deployment, we cold sterilized VITs for 24 hours in Nolvasan solution (Fort Dodge Animal Health, Fort Dodge, IA), rinsed them with sterile saline, and stored them individually in sterile Whirl-Pak bags (Nasco, Modesto, CA). We placed VITs in a sterile disposable, lubricated speculum (Animal Reproductive Systems, Chino, CA), which was inserted in the vagina to the cervix at capture. We held VITs in place at the cervix with a 19-mm diameter polyvinyl chloride (PVC) tube as the speculum was slowly pulled back. We discarded disposable speculums, washed the smaller diameter PVC tube with soap and water, and cold sterilized PVC tubes in Nolvasan solution between deployments. Moose normally shed the VITs at parturition and the pulse rate changed from 40 PPM to 80 PPM when the temperature dropped below 32° C. In addition to the pulse rate change, the VITs emitted a coded pulse that enabled us to determine how long each had been shed, in increments of 30 minutes, for periods of up to 5.5 days. The Trent University Animal Care Committee and the Ontario Ministry of Natural Resources approved all capture and handling methods (Permit Nos. 06–66, 07–66, 08–66, 09–66).

We aerially radiotracked VIT-equipped adult female moose biweekly following capture until early-May when daily monitoring began. At the onset of calving, we monitored these moose daily with aerial or ground telemetry to determine calving status. When a VIT was shed, a crew of 2–4 used hand-held antennas and portable receivers to locate the calving site. Ballard et al. (1979) suggested that some study-induced calf abandonments by moose resulted from calves being handled before an adequate cow–calf bond had formed. Accordingly, we refrained from visiting birth sites of calves until the coded VIT pulse indicated calves were ≥10 hours old. If a calf (or calves) had already left the birth site, we used the cow's location as the center of the search area and assumed that the calves moved in her direction. If we did not find calves immediately, we expanded the search area to a 100–200-m radius around the birth site. When we spotted a calf, we attempted to capture it by hand and collar and process it as described above.

Monitoring of Collared Calves

We attempted to monitor calves daily during the first month of life and ≥twice a week for the remainder of the summer. Thereafter, we monitored most calves ≥once a week until they either died or exited the study on their first birthday. When we detected a mortality signal, we recovered the collar and any remains, and determined cause of death using evidence at the mortality site (Ballard et al. 1979). Specifically, we collected hair and scat samples, inspected tracks, examined carcasses for puncture marks and wounding patterns, and took photographs. When we found sufficient remains, we submitted them for full necropsy at the Canadian Cooperative Wildlife Health Centre (CCWHC), University of Guelph, Ontario.

Survival and Hazard Modeling

We estimated annual survival probabilities using the Kaplan–Meier product-limit estimator, modified by Pollock et al. (1989) to allow the staggered entry of animals. We entered calves into the analyses on the day after radiocollaring and removed them when they died, or were censored because of dropped or failed collars. We censored all surviving calves from the analysis when they reached 1 year of age. We assessed whether survival distributions differed among years using Wald's test (Therneau and Grambsch 2000). To estimate rates of cause-specific mortality, we generated the non-parametric cumulative incidence function estimator (NPCIFE) using the SPLUS code presented by Heisey and Patterson (2006). We considered 3 competing risks: 1) human harvest, 2) predation, and 3) other natural causes of death (included malnutrition, exposure, winterkill, or parasite mortality). To further illustrate temporal changes in risk of mortality for calves, we estimated the penalized likelihood estimate (PLE) of the instantaneous hazard ($h_{(t)}$) using program PHMPL (Joly et al. 1998, 1999). The hazard function illustrates changes in instantaneous rate of death over time (in this case across the biological year) for the population in question. We allowed PHMPL to determine the smoothing parameter automatically.

We used Anderson-Gill proportional hazards models (DelGiudice et al. 2002) to assess the influence of study area, year, and weight at collaring on the risk of succumbing to the specific causes of mortality identified above as described by Lunn and McNeil (1995) and Heisey and Patterson (2006). All rates are presented as mean ± standard error unless otherwise noted. To assess the degree to which hunting mortality was additive to other mortality factors, we compared total mortality among the hunted and unhunted populations. We considered mortality to be additive if total mortality rates differed between populations by an amount similar to the hunting mortality rate. Alternatively, similar overall mortality rates between populations (despite hunting only being present in 1 area) would suggest that hunting mortality was largely compensated for by reductions in the magnitudes of other natural mortality factors.

RESULTS

Twinning Rates and Capture Success

We deployed 86 of the 99 VITs in cows later determined to be pregnant. We were able to determine calving success during the subsequent year for 5 of 13 cows that carried their VITs beyond the year of deployment. Of those, 4 successfully calved during the subsequent calving season, whereas the VIT in the 5th cow became encapsulated in fibrous tissue and a veterinarian member of the capture crew was unable to safely remove it upon recapture the subsequent winter. Serum progesterone levels indicated she was not pregnant at the time of this subsequent examination. We were unable to determine subsequent calving status of the remaining 8 cows that were not pregnant at the time of VIT deployment because their collars either failed or dropped prior to the next winter capture session ($n = 4$), or because the study ended prior to the subsequent calving season (2010; $n = 4$).

Twinning rates averaged 12.5 ± 0.9% in WMU49 ($n = 40$ calving events) and 20 ± 0.3% in APP ($n = 50$ calving events). These rates were not significantly different (Fisher's exact test, $P = 0.262$) and produced an overall twinning rate of 16.7 ± 0.4% across the 2 study areas. We documented 4 cases of stillborn calves among 84 recent (<48 hr following parturition) birth sites investigated (2 in each study area; $\bar{x} = 4.7 \pm 0.3\%$) and a single case where the radiocollared dam died during birthing (APP).

We successfully captured and radiocollared 87 neonatal calves (46 in APP and 41 in WMU49; Table 1). Two calves slipped their collars within a week of collaring; all others kept their collars for >1 month unless they died sooner. We located all but 2 of the calves collared in APP without use of VITs either by monitoring movements of radiocollared cows ($n = 4$ birthing events) or by searching known calving areas ($n = 35$ birthing events), whereas we located all calves collared in WMU49 by monitoring radiocollared cows fit with VITs (Table 1). We collared calves in WMU49 a median of 19 hours after birth (range = 9.5–58 hr). In APP, we estimated 48% of the calves to be <48 hours old at time of collaring, whereas the remaining 52% were estimated to be 48–120 hours old at collaring. Examination of known-aged calves indicated close corroboration with the criteria presented by Larsen et al. (1989) for aging moose calves. We assumed that 4 calves that died of unknown causes <48 hours after collaring in WMU49 were abandoned. In all 4 cases, we recovered the carcasses <12 hours after death and the radiocollared dams survived until the end of our study. We assumed abandonment was the cause of death because none of these calves had any discernible milk in their stomachs nor was any other likely cause of death identified during the post-mortem examinations at the CCWHC. Although we are confident that these calves were abandoned, we cannot be certain whether the abandonment was a direct result of our handling (Powell et al. 2005). Two of these calves had high birth weights (16 kg and 17 kg vs. a mean weight of 15.4 ± 0.3 for all calves captured within 48 hr of parturition), whereas the remaining 2 were light (12 kg and 13.5 kg). None of these abandoned calves were twins, but 2 were born to the same dam during subsequent years. Despite the uncertainty regarding the role our handling played in the death of these calves, given the precedent established by previous studies (e.g., Ballard et al. 1979, Keech et al. 2011), we censored these 4 calves, resulting in a sample of 81 calves for further analyses (44 in APP and 37 in WMU49).

Calf Survival

Annual survival averaged 63.7 ± 7.1% (Fig. 2), was higher in APP (72.1 ± 6.8%) than WMU49 (55.1 ± 8.3%; $Z = 2.15$, $P = 0.032$), and was higher in 2009 relative to 2006–2008 ($Z = -2.2$, $P = 0.028$). Despite the higher survival in 2009, we pooled data among all years of study for further analyses because of small sample sizes. Calves in both study areas experienced the greatest instantaneous mortality risk during the first month of life (Figs. 2 and 3) and calves in WMU49 experienced another pronounced increase in mortality risk during the autumn hunting season (Fig. 3).

Including the 4 cases of probable abandonment, we documented 32 mortalities during the first year of life among the collared calves (Table 2). The relative influence of different causes of mortality clearly differed between study areas. Hunting only occurred in WMU49 and removed 15.9 ± 0.058% of calves annually. Ten of the 13 documented cases of predation on calves occurred in APP ($M_{\text{pred}} = 0.233 \pm 0.062$ vs. 0.090 ± 0.036 in APP and WMU49, respectively; $\chi^2 = 5.03$, $P = 0.025$). Predation was the largest source of mortality for calves in APP ($\chi^2 = 8.45$, $P = 0.004$). Bears and wolves killed 7 and 6 collared calves, respectively, with bear predation being largely confined to early summer, whereas the hazard of being predated by wolves extended into winter (Fig. 4).

Deaths due to natural causes other than predation, such as malnutrition and exposure in spring, and malnutrition or tick-related mortality in winter, were rare in APP ($M_{\text{nat}} = 0.0467 \pm 0.032$) but common in WMU49 ($0.200 \pm 0.054$, $\chi^2 = 6.57$, $P = 0.010$). The overall annual mortality rate was greater in WMU49 (0.170) by an amount similar to the hunting mortality rate (0.159), suggesting hunting may have been largely additive to other mortality factors. Considering calves from both study areas combined, weight at collaring had no effect on risk of mortality by predation ($Z = -0.156$, $P = 0.88$), but each additional kg of weight decreased risk of succumbing to other causes of natural mortality by 33% ($Z = -2.5$, $P = 0.011$). Risk of dying of abandonment or malnutrition or exposure during the first week of life also decreased marginally with weight at

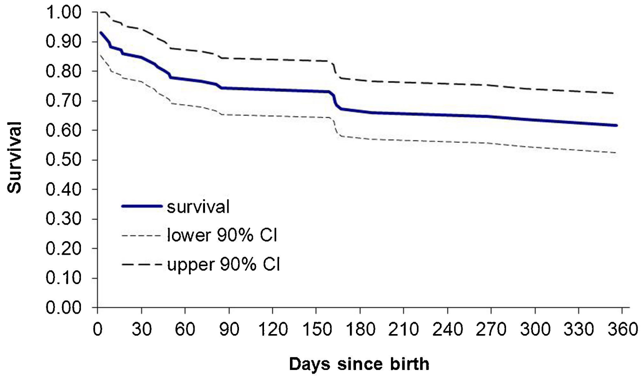

Figure 2. Annual survival distribution of 83 moose calves collared during 2006–2009 in central Ontario, Canada.

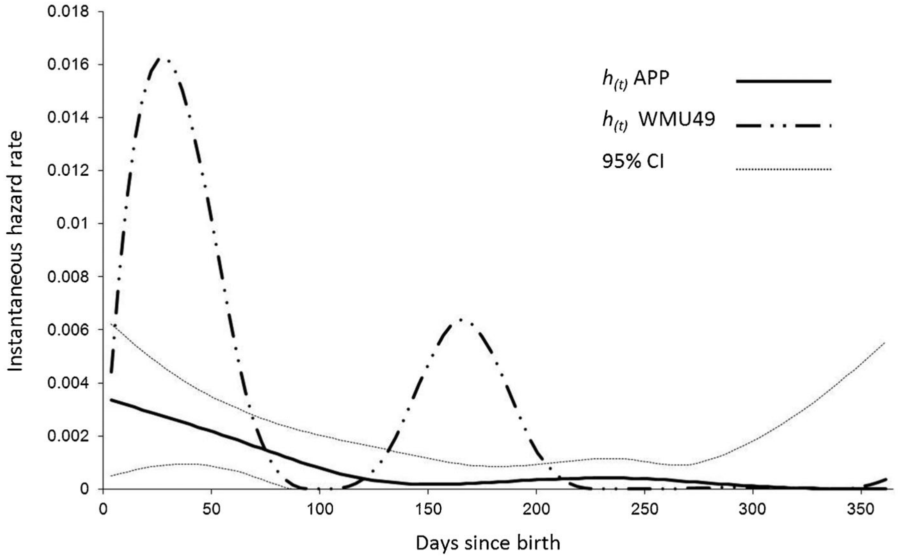

Figure 3. Seasonal changes in the penalized likelihood estimate (PLE) of the hazard, $h_{(t)}$ (95% CI), for 44 and 39 moose calves monitored in Algonquin provincial park (APP) and Wildlife Management Unit 49 (WMU49), respectively, in central Ontario, Canada, 2006–2009. The PLE depicts changes in instantaneous rate of death over time.

collaring (risk ratio = 0.913 ± 0.054, $Z = -1.82$, $P = 0.069$).

DISCUSSION

We documented calf survival rates (0.637) that were approximately 50% greater than those documented in northeastern Minnesota where wolves and black bears were also present (0.404; Lenarz et al. 2010), and in northern New Hampshire where black bears were the only substantive predator of moose calves (0.45; Musante et al. 2010). Calf survival in areas inhabited by brown bears (*Ursus arctos*) ranged from 0.20 to 0.35, with most losses occurring during the first month following birth (Boertje et al. 1988, Larsen et al. 1989, Ballard et al. 1991, Ballard and Van Ballenberghe 1998, Bowyer et al. 1998, Testa et al. 2000). Similarly, in northeastern Alberta where wolves were responsible for 29% of losses, the annual survival rate of calves of radiocollared dams was 0.27 (Hauge and Keith 1981).

Major limiting factors for moose calves differed between the protected and unprotected landscapes we studied. Hunting of moose only occurred in WMU49, but despite over-the-counter access to moose calf hunting licenses, and 50% of the WMU being relatively accessible public land, hunting only removed about 16% of calves each year (90% CI = 6–26%). The compensatory mortality hypothesis predicts that increased predation or harvest mortality reduces competition for resources and elicits a density-dependent reduction in natural mortality (Boyce et al. 1999) and was the basis for the present moose harvest system in Ontario (Euler 1983). However, our results suggest that hunting mortality was largely additive to other mortality factors. Also, for increases in a particular mortality factor to be compensated for by reductions in other mortality factors, the mortality factor to be compensated for must occur prior to those other factors. Consistent with other studies, only 14% of non-abandonment-related deaths occurred after the autumn hunting season (Figs. 2–4), suggesting limited opportunity for compensatory reductions in natural mortality.

The disparity in predation we observed between study areas was likely due to reasons more complex than simple differences in predator abundance. Although bear densities were similar between the 2 study areas, hunting, which only occurred in WMU49 and was skewed towards males (McLaren et al. 2009), may have altered both the sex and age ratios of the bear population and resulted in fewer large bears capable of successfully preying on moose calves. Indeed, among black bears, large males are generally considered the most likely to kill large prey (Gunther and Renkin 1990,

Table 2. Causes and rates of mortality of neonatal moose calves in Algonquin provincial park (APP) and Wildlife Management Unit 49 (WMU49) in central Ontario, Canada, 2006–2009.

	APP		WMU49	
Cause of death	**Rate**	**SE**	**Rate**	**SE**
Hunting			0.159	0.058
Predation	0.233	0.062	0.090	0.036
Other natural causes[a]	0.046	0.032	0.200	0.059
Total mortality	0.279		0.449	

[a] Includes primarily deaths due to malnutrition or exposure in spring, and malnutrition or tick-related mortality in winter.

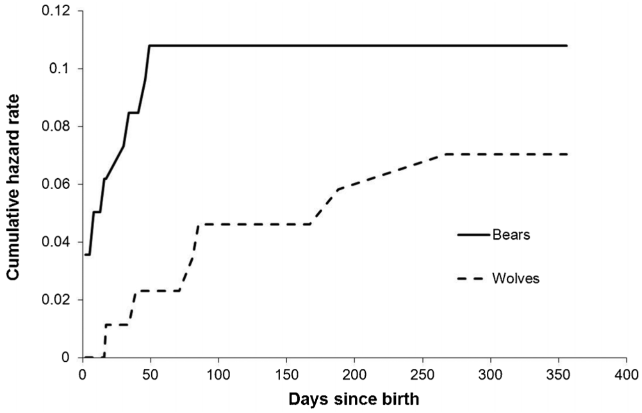

Figure 4. Cumulative probability of predation by bears or wolves for 83 moose calves monitored in central Ontario, Canada, 2006–2009.

Jacoby et al. 1999). Adult female black bears do prey on moose calves, but a defensive cow moose can be dangerous prey for the much smaller adult female black bears (Obbard et al. 2000). Such predation attempts are likely less risky for the much larger adult male black bears that can even prey successfully on adult cow moose (Austin et al. 1994). Therefore, a black bear population with a smaller proportion of adult males might exert less predation pressure on the moose population.

Wolves were moderately abundant in APP (2.3–3.0/ 100 km^2; Patterson et al. 2004), and although wolf-like canids were likely even more abundant in WMU49, most free-ranging canids in the area were eastern coyotes and wolf–coyote hybrids (Benson et al. 2012) that seemed to be less effective predators of moose calves (J. Benson and B. Patterson, OMNR, unpublished data).

If moose in APP calve on islands and peninsulas as a means of reducing contact with black bears as suggested by Addison et al. (1990), our reliance on searching these areas to collar calves may have led to a biased sample. We may have further underestimated predation rates in APP because of the slightly older age at collaring of most calves in APP relative to those captured using VITs in WMU49. However, we did not locate consumed remains or fresh bear scats indicative of predation of uncollared neonates during 4 years of intensive searching of traditional calving areas in APP, but did find 2 unscavenged stillborn calves, suggesting this was not the case. Regardless, if our sample of calves from APP resulted in a low-biased estimate of early predation rates, the actual differences in predation between study areas were even more pronounced than we estimated.

Deaths due to non-predator related natural causes, such as malnutrition and exposure in spring, and malnutrition or tick-related mortality in winter were rare in APP but were an important source of mortality in WMU49. Although sample sizes were low, the data suggest that the lower predation rates on calves in WMU49 may have been partially compensated for by increases in other natural mortality factors. Indeed, the non-predator natural mortality rate was 4× greater in WMU49 relative to APP (Table 2). In western Interior Alaska, non-predation mortalities of calves similarly increased following predator removals (Keech et al. 2011). A recent review of moose population trajectories relative to climate and landscape cover suggests that the onset of the growing season is an important determinant of moose calf recruitment in Ontario (Brown 2011). We suggest that the ultimate effects of climate may be mediated through calf vigor during summer and increased prevalence of brainworm (*Parelaphostrongylus tenius*), giant liver fluke (*Fasciolodes magna*), and potentially winter tick (*Dermacentor albipictus*) owing to warming temperatures and the associated high densities of sympatric deer (Murray et al. 2006, Lenarz et al. 2010, Musante et al. 2010). However, greater rates of natural mortality in WMU49 may also have reflected lower maternal investment among cows in this area. Maternal defense of calves was nearly absent in WMU49, with most cows retreating when they first observed our approach. In APP, maternal defense became increasingly common during the course of our study, to the extent that by 2008 we were unable to collar the calves of most VIT-equipped cows because of strong maternal aggression. Whether this difference in maternal defensive behavior reflected a response to hunting by humans in WMU49 or greater predation pressure by wolves and bears in APP is unclear (see below for further discussion). Regardless of the cause, aggressive behavior by cows limited the effectiveness of VITs as a means of collaring newborn calves in APP. Unlike Alaskan studies that used helicopters to separate aggressive cows from their calves, we encountered many of these cows in mature deciduous forests where a helicopter would have been ineffective. We were reluctant to routinely dart and drug the cows because of concerns for the calf being crushed by a falling cow, or trampled by a recovering cow (e.g., Garner and Addison 1994), although we did successfully sedate a defensive cow with xylazine HCL (Cervizine 300®; 300 mg/cm^3, Wildlife Pharmaceuticals, Windsor, CO) at approximately 3 mg/kg body mass (CAZWV 2009) and reversed the xylazine with atipamezole hydrochloride (Antisedan; Pfizer Bio-Pharmaceuticals and Animal Health, Mississauga, Ontario, Canada).

The 4 calves that we suspect were abandoned in WMU49 represented 9.3% of the calves handled in that study area and 4.6% of all calves handled. Ballard et al. (1979) reported abandonment-related losses of 13.2% among 197 newborn calves collared in Alaska during 1977–1978. We observed all suspected capture-related abandonments, a greater prevalence of non-predation natural mortality factors, and little to no maternal defense in WMU49, suggesting the possibility of lower maternal investment in this area. We are unclear why dams would exhibit lower maternal defense in WMU49, which had less predation pressure and therefore less risk to dams in protecting their calves. Keech et al. (2011) reported abandonment-related losses of 11% of captured calves following predator control versus 1% of calves similarly lost during the pre-predator control phase of their study. They also reported that dams defended calves less vigorously in later years of the study, particularly when females were nutritionally stressed following difficult winters. The lower maternal defense we observed in WMU49 relative to APP, and that observed by Keech et al. (2011) following predator control, may have been primarily due to either low predation pressure or poorer nutritional condition of dams owing to density-dependent forage competition.

Our results suggest greater estimates of calf recruitment than estimated during calf-at-heel counts conducted during moose aerial surveys in both study areas (0.20–0.40 calves/cow in mid-winter; Brown 2011; OMNR, unpublished data). Calf-at-heel surveys may provide a useful index of calf recruitment over time but can be inconsistent and misleading owing to visibility bias and a lessening of cohesiveness of calves to their mothers as they mature (Bonenfant et al. 2005, Gundersen et al. 2008). A further limitation of calf-at-heel counts is the inability to identify specific causes of mortality. For example, given the proximity of our 2 study areas and the similar landscape and environmental conditions, without radiocollared calves one might have erroneously concluded that the same limiting factors were similarly influencing calf survival in the 2 study areas. Conversely, studies such as ours that require capture, radiocollaring, and aerial monitoring of dams and calves are much more expensive, labor-intensive, and invasive than simple aerial surveys. Even in a study area with reasonable ground access, during our most successful field season, we were only able to capture calves belonging to 74% of the pregnant dams fit with VITs (WMU49 in 2009; Table 1). In the worst-case scenarios (APP, 2007–2008) we were unable to capture any calves belonging to dams fit with VITs because of remote calving sites and strong maternal aggression. Researchers interested in investigating moose calf mortality must consider the high cost and logistical difficulty of collaring statistically relevant sample sizes of newborn calves in forested areas using radiocollared dams fit with VITs.

Another important consideration is the invasiveness of capturing and radiocollaring both neonates and dams, and the potential for capture-related mortalities and injuries. Installation of VITs presents an additional ethical consideration. We did not have access to a portable ultrasound and were unable to assess pregnancy prior to deployment of VITs. However, given the relatively liberal calf harvest regulations, the low calf-at-heel counts, the perception that hunting and/or predation was negatively influencing calf recruitment, and poor population performance of moose along much of their southern range, collecting the survival data on calves was important. Regardless, our inability to confirm pregnancy prior to deploying VITs not only reduced our efficiency but also resulted in 13 of the 99 cows we fit with VITs carrying their VITs for ≥ 15 months. Fortunately, carrying VITs beyond the year of deployment caused no known mortalities and did not inhibit future reproduction in 4 of the 5 cases we were able to monitor. Nonetheless, a 20% sterility rate (i.e., 1 in 5) is unacceptable, and for both ethical and efficiency purposes, future research involving fitting of any animal species with VITs should make every effort to confirm pregnancy a priori. In cases where this is not possible, researchers must carefully consider the risk of injury or discomfort to animals against the need to acquire the resulting data.

MANAGEMENT IMPLICATIONS

Restrictions on hunting and predator control are commonly invoked to promote population growth of harvested moose populations. Although managers typically assume that harvest of juvenile ungulates prior to their first winter is largely compensatory, because most moose hunting seasons occur after much of the non-hunting mortality of calves has occurred, other mortality factors have little potential for compensatory reductions. Furthermore, calves generally predominate among moose predated by wolves in winter (Nilsen et al. 2005, Gervasi et al. 2012, Sand et al. 2012). By reducing the proportion of juveniles in the pre-winter population of moose, hunting of calves may shift predation pressure to demographically more important segments of the population such as mature cows and bulls. Although over-harvest of calves in WMU49 seems unlikely, managers in jurisdictions with more substantive predators, or extensive access for hunters, should consider the potential additive effects of calf hunting cautiously when contemplating changes to moose hunting regulations. Furthermore, although predation on moose calves is also generally a largely additive mortality factor (e.g., Sand et al. 2012), lower maternal defense and a greater incidence of natural mortality of calves in areas with lower predation pressure suggests a dampened benefit of predator control on moose population growth (but see also Keech et al. 2011). Finally, future research should explicitly assess the effects of habitat improvements on nutritional condition of dams, their subsequent care and defense of their calves, and ultimately increased calf recruitment into the adult population.

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