Big enough for bears? American black bears at heightened risk of mortality during seasonal forays outside Algonquin Provincial Park, Ontario

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Big enough for bears? American black bears at heightened risk of mortality during seasonal forays outside Algonquin Provincial Park, Ontario

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Abstract: Protected areas may provide insufficient protection for carnivores such as bears (Ursidae) with large home ranges and extensive seasonal movements. Even in protected areas, harvest can be the main cause of mortality if parks are small or individuals live close to the boundary. At >7,600 km^2, Algonquin Provincial Park (APP) is the largest protected area in southern Ontario, Canada, yet wolves (*Canis lycaon c.f.*) experienced increased mortality when leaving APP to hunt white-tailed deer (*Odocoileus virginianus*). American black bears (*Ursus americanus;* hereafter, bears) also undertake seasonal movements, and may incur increased risk of harvest related mortality if they leave the park. We fitted 72 bears with Global Positioning System or Very High Frequency radiocollars during 2006–2014 to determine overall and cause-specific mortality rates, and whether risk of mortality changed when bears left APP or during years of low natural food availability. Further, we compared the abundance of resident bears with harvest rates in Wildlife Management Units (WMUs) surrounding APP to determine whether harvest was higher in areas surrounding the park compared with WMUs farther from the park boundary. Hazard analysis showed annual mortality for radiocollared bears in APP was 15%. Harvest mortality was double that of all other causes combined. Bears were 7 times more likely to die outside the park. Years of lower natural food availability inside the park, or higher red oak (*Quercus rubra*) availability outside the park did not significantly alter the risk of mortality. Male bears were 6 times more likely to be harvested than females, and 4 times more likely to die from other causes. High harvests of bears in WMUs near APP contrasted with low abundance of resident bears, suggesting that APP acts as a source population for harvest that occurs near park boundaries. Meaningful maintenance of the integrity of bear populations in protected areas should be undertaken at the landscape scale.

Key words: Algonquin Provincial Park, American black bear, hazard analysis, mortality, Ontario, park, protected areas, survival, *Ursus americanus*

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For large carnivores living in protected areas, the risk of population decline or extirpation is greater for animals with larger home range sizes because wide-ranging movements often bring the animals in closer contact with humans outside the boundary of the protected area (Woodroffe and Ginsberg 1998). In areas where human density is high, there is an increased probability of a decline in abundance of large carnivores or even local extirpation, although human tolerance for carnivores varies greatly (Woodroffe 2000). In eastern North America, most protected areas may be too small to provide adequate protection for resident mammals within their boundaries and avoid loss of species (Gurd et al. 2001). Bears (Ursidae) may be particularly vulnerable because of their life-history characteristics and wide-ranging movement patterns, which often take them outside protected areas. Key traits that can result in increased

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risk of population decline include low reproductive rates combined with large body size and frequent interactions with humans (Cardillo et al. 2005).

Paradoxically, human-caused mortality, including hunting, is often the main cause of death for bears living in protected areas (Woodroffe and Ginsberg 1998). Other types of human-caused mortality such as defense of life and property removals or roadkills also may be important factors affecting survival (Bischof et al. 2009). For example, grizzly bears (*Ursus arctos*) had increased mortality risk outside Yellowstone National Park where road density was high (Johnson et al. 2004). Although bears may select habitat that minimizes human-caused disturbances (Martin et al. 2010), years of low natural food availability are associated with increased levels of human–bear conflict (Howe et al. 2010, Obbard et al. 2014). If bears regularly leave the confines of a protected area to forage outside the protected area, harvest or defense of life and property kills may be a significant, or even major, cause of mortality.

In Ontario, Canada, the guiding legislation for Ontario Parks, the *Provincial Parks and Conservation Reserves Act, 2006* (PPRCA; Provincial Parks and Conservation Reserves Act, 2006, S.O. 2006, c. 12, https://www.ontario.ca/laws/statute/06p12, accessed 1 Aug 2016), includes ecological integrity as the first priority in guiding all aspects of the planning and management of Ontario's system of provincial parks and conservation reserves. The PPRCA defines ecological integrity as "a condition in which biotic and abiotic components of ecosystems and the composition and abundance of native species and biological communities are characteristic of their natural regions and rates of change and ecosystem processes are unimpeded" (PPRCA 2006, c. 12, s. 5 (2)). In plain language, the PPRCA guiding philosophy is that an ecosystem has integrity when the animals, plants, and non-living parts such as soils and water are functioning and interacting naturally and these interactions are not changed by human activity. The heart of this definition describes a healthy, naturally functioning protected area. Maintaining ecological integrity is an important concept in park management in Ontario.

From mid-summer to autumn, American black bears (*U. americanus;* hereafter, black bears) typically make seasonal migrations to areas of food concentration outside their home range, distances that are often >25 km and that may be >200 km (Garshelis and Pelton 1981, Rogers 1987, Obbard and Kolenosky 1994, Hellgren et al. 2005, Noyce and Garshelis 2011, Noyce and Garshelis 2014). Bears typically travel to areas with more abundant or concentrated food sources (Rogers 1987, Obbard and Kolenosky 1994, Noyce and Garshelis 2011). Years of lower local food availability may cause an increase in the percentage of bears that make seasonal migrations. In Algonquin Provincial Park (APP), the largest protected area in Ontario south of the boreal forest, adult female black bears undertake seasonal forays in late summer or autumn to areas outside the Park where bear hunting occurs (Maxie 2009); therefore, they may be at heightened risk of mortality when outside the protected area.

Our objectives were to characterize the risk of mortality for black bears living in Algonquin Provincial Park. To do this we determined (1) the distribution and number of resident bears compared with harvested bears in the Wildlife Management Units (WMUs) surrounding APP, (2) overall survival for black bears in APP, (3) cause-specific mortality for black bears in APP, and (4) how risk of mortality changed when bears left APP and in years of low natural food availability. Based on the above, we assessed whether APP affords adequate protection to resident black bears.

We hypothesized that APP-resident black bears were subsidizing the harvest numbers outside the park when they were killed during late-summer forays beyond park boundaries; and, as a consequence, the number of harvested bears compared with the resident bear population would be higher in WMUs immediately outside APP compared with WMUs farther from APP. Further, we predicted that the density of resident bears around APP would be low due to historical harvest pressure close to the park boundary. We expected that overall survival for black bears in APP would be at a sustainable level because the park would be large enough to protect resident bears, but also that harvest would be the main cause of death for APP bears. Finally, we hypothesized that risk of mortality would increase significantly when bears left APP, and in years of lower food availability inside the park or greater food availability outside the park.

Study area

Algonquin Provincial Park (45°27′N, 78°27′W) was established in 1893 as a forest reservation, fish and game preserve, and recreational area (Killan 1993). At approximately 7,600 km^2 (Fig. 1), APP is the largest protected area in central Ontario. The park is larger than the estimated minimum area required to conserve species richness of mammals in reserves in eastern North America without additional management of populations or critical habitat (Gurd et al. 2001). Timber harvest occurs via selection and uniform shelterwood systems, with a small

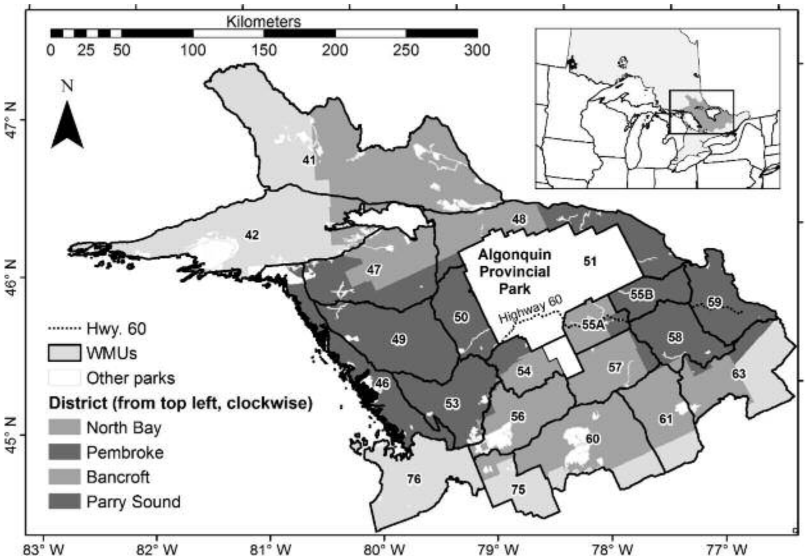

Fig. 1. Algonquin Provincial Park and surrounding Wildlife Management Units (WMUs) and Ontario Ministry of Natural Resources administrative districts in Ontario, Canada. Inset shows location within the province.

amount of clear-cutting for shade-intolerant species in the east side of the Park (Algonquin Forestry Authority 2005). Public access to APP is largely through the only paved road (Highway 60), which runs through the southern half of the park (Fig. 1).

Algonquin Provincial Park is part of the Great Lakes–St. Lawrence Forest Region (Rowe 1972) and the boreal forest Ecozone (Ecological Stratification Working Group 1995), a transitional zone between the largely coniferous forests to the north and broadleaf forests to the south. Our study was focused in the western portion of APP where hilly, rocky upland forests are characterized by species such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), red maple (*A. rubrum*), eastern hemlock (*Tsuga canadensis*), and balsam fir (*Abies balsamea;* Quinn 2004). Western APP reaches elevations of 580 m above sea level; mean temperatures during the study were −10.5°C and 17.8°C in January and July, respectively (Environment Canada, 2015).

Approximately 2,200 black bears reside in APP (Howe et al. 2013; M.E. Obbard, unpublished data). Hunting for any species is prohibited with the exception of the southern portion of the park in WMU 54 (Fig. 1), and the hunting of moose (*Alces alces*) by members of the Algonquins of Ontario First Nation in the central and eastern areas of the park (Ontario Ministry of Natural Resources 1998). In WMUs surrounding APP, the open season for black bears during our study was from 1 September to 30 November each year and bag limit was 1 bear/license.

Methods

Distribution of bears and bear harvest around Algonquin Provincial Park

To determine whether harvest was disproportionately higher around APP, we compared 2 indices (black bear density and harvest index) representing the number of resident and harvested bears for WMUs near APP (Tier 1) with WMUs farther away from APP (Tier 2) using 1-sided tests; we expected resident bear populations to be higher in Tier 2 and harvest to be higher in Tier 1. Tier 1 WMUs were within the greatest distance traveled by any Global Positioning System- (GPS-) collared bear from the park boundary (53 km). Tier 2 WMUs were any WMUs that shared borders with Tier 1 WMUs. We determined distance to park edge for each WMU by averaging all pixels in a 100 × 100-m Euclidean distance raster to the APP boundary (ESRI 2010). With the exception of WMU 49, no Tier 2 WMUs were visited by GPS-collared bears, whereas all Tier 1 WMUs were used by GPS-collared bears.

Densities of resident adult female black bears were previously estimated for all WMUs based on data from non-invasive DNA sampling from 2004 to 2010 and spatially explicit capture–recapture models (Obbard et al. 2010b, Howe et al. 2013). Non-invasive sampling in these studies was completed before early July each year (i.e., before bears might leave on seasonal forays to late-summer or autumn foraging areas and before subadults might be expected to disperse); therefore, the resident population was sampled. We used estimates of total density and population size, including cubs and yearlings, using the expected age distribution calculated from demographic information obtained from long-term studies of black bears in Ontario (Yodzis and Kolenosky 1986, Kolenosky 1990, Obbard and Howe 2008). Densities were calculated based on suitable bear habitat within the WMU (i.e., excluding large water bodies, agricultural areas, and areas of human habitation).

We averaged harvest metrics for 2006–2014. We calculated projected harvest for each WMU by summing (1) the number of black bears reported harvested through mandatory reporting for resident bear hunters multiplied by the reporting rate (the no. of licenses issued divided by the no. of valid replies), (2) the number of bears taken using a second seal (issued for some WMUs where local ministry staff determined that they could sustain increased harvest pressure) multiplied by the reporting rate, and (3) the number of bears harvested by non-residents as reported through the black bear license validation certificate (Dix-Gibson 2015). For resident hunters in Ontario, the reporting rate is known to be lower than actual harvest due to non-reporting, whereas all non-resident hunters must report harvest and compliance is high. We divided the projected harvest by the estimated number of resident bears to represent percent projected harvest. We ensured data met the assumption of normality or transformed data to meet that assumption before comparing density and harvest estimates between Tier 1 and Tier 2 WMUs using a Student's *t*-test with Satterthwaite degrees of freedom in Program R version 3.2.4 (R Core Team 2016).

Bear capture

From mid-May to late August 2006–2014, we captured 72 black bears (Table 1) in barrel or culvert traps and chemically immobilized individuals using methods outlined in Obbard et al. (2010a). Study areas were in APP within 20 km north and south of the Highway 60 corridor (Fig. 1). We assessed age of bears based on counts of cementum annuli of the first premolar tooth, taking into account the sex of the bear (Stoneberg and Jonkel 1966, Coy and Garshelis 1992). All capture and handling procedures were approved annually by the Animal Care Committee of the Ontario Ministry of Natural Resources and Forestry (permits 06-21, 07-21, 08-21, 09-21, 10-21, 11-21, 12-21, 13-21, 14-21). Handling procedures followed the general guidelines of the Canadian Council for Animal Care (Canadian Council on Animal Care 2003) and the American Society of Mammalogists (Sikes and Gannon 2011).

We attached individually numbered aluminum or plastic ear tags to each black bear. Tags were inscribed with a contact telephone number (aluminum tags) or a notice reading "CALL BEFORE EATING" and the contact telephone number for the "Bear Wise" program, an Ontario Ministry of Natural Resources and Forestry program intended to reduce human–bear conflicts (Ontario Ministry of Natural Resources and Forestry 2015). We deployed GPS radiocollars (Lotek models 3300L, 4400M, or Iridium; Lotek Wireless, Newmarket, Ontario, Canada) on 31 bears $\geq$3 years old (Table 1) and scheduled the collars to obtain location fixes every hour or every half hour, depending on year. We removed fixes from the database if they had a Keating's index $>$10 (Keating 1994). We deployed Very High Frequency (VHF) collars (Lotek Wireless) on 55 bears, including yearlings; during the study, we changed 13 of these bears from carrying VHF collars to GPS collars. All collars were inscribed with a contact telephone number.

We assumed that we were aware of most human-caused deaths of black bears in our study because we were contacted about the fate of all harvested GPS-collared bears. In one case, a collar was tracked to beneath a frozen lake and data were never recovered, but otherwise all GPS collars were retrieved. Natural deaths of VHF-collared bears were less likely to be discovered because only bears that died in the park within range of truck-mounted telemetry equipment used on navigable roads routinely would be detected. To counteract this, we conducted monthly aerial telemetry flights in fixed-wing aircraft during late summer and autumn to find bears that had dispersed outside this range and determine their fate.

Annual survival

We used the generalized Kaplan–Meier method and a null Anderson–Gill proportional hazards model to calculate total annual survival, S(*t*), 2006–2014 (Heisey and Patterson 2006) for 31 GPS-collared black bears. We entered bears into survival models on the day following the day they were captured and we right-censored bears when radiocollars were turned off for the winter hibernation period (always by 16 Dec). We re-entered bears into the risk set the day GPS radiocollars were activated in the spring (always after 14 Mar). We did not include bears in the risk set when they were not actively monitored for part of the season as a result of a dropped or failed

Table 1. Sample size and number of deaths for male and female American black bears (*Ursus americanus*) collared in Algonquin Provincial Park, Ontario, Canada, 2006–2014. GPS, Global Positioning System; VHF, Very High Frequency.

Sex	Age class	GPS-collared bears		VHF- and GPS-collared bears	
		N	Deaths	*N*	Deaths
F	Ad	22	8	23	9
	Subadult	8	0	15	1
	Yearlings	0	0	16	1
	F total	30	8	54	11
M	Ad	4	1	7	3
	Subadult	5	3	12	4
	Yearlings	0	0	16	3
	M total	9	4	35	10
	Grand total	31[a]	12	72[a]	21

[a]Some bears changed age classes during the study; therefore, the grand total reflects the number of individuals in the study, not the total no. of males and females of all age classes.

collar. If we re-captured bears, we re-entered them into the risk set the day of re-capture. Bears that were previously collared with a VHF collar were entered into the models either the day the collar was switched to a GPS collar or when the GPS collar was activated in the spring. We right-censored bears when a collar was dropped ($n = 4$), failed ($n = 2$), switched to a VHF collar ($n = 3$), or the collar was removed before the end of the study ($n = 2$). We assumed that censoring was independent of fate, especially because many collars failed or dropped during or immediately following the winter denning season, presumably due to collars loosening over the season as bears lost weight.

We did not follow VHF-collared black bears as frequently as GPS-collared bears, so we conducted a separate analysis to calculate survival for VHF- and GPS-collared bears combined. Between May and August, we typically located VHF-collared bears 3–7 times/month. We included bears in the risk set only if we located them $\geq$1 time per month during May–August after entering the risk set. During September–November, we typically located bears 1–2 times/month. We assessed survival of most bears during winter visits or by re-capturing them in the spring. Therefore, we allowed bears without locations in September–November to remain in the risk set until 30 November of a given year only if we observed them the following winter during den visits or by June the following spring; otherwise, we censored them on their last observed date in the summer or autumn. To account for the coarser nature of these data compared with that of GPS-collared bears, we used week as the time variable in the survival models instead of day. We acknowledge the problems associated with dispersing VHF-collared bears becoming censored in the analysis that could result in survival estimates being biased upward. However, the addition of 41 individuals to the survival models enabled us to estimate the influence of sex and age on risk of mortality. In a study with 101 bears and 34 mortality events, Obbard and Howe (2008) showed that total survival rate for the same data set of bears differed by only 3.2% when comparing between a censored data set and a data set where bears were assumed to have died when contact was lost. Given that it is unlikely that all censored bears died, error in the present study is likely smaller than this. Global Positioning System–collared bears were frequently adult females, whereas VHF-collared bears were generally adult males or subadults and yearlings of both sexes. We provide annual survival estimates for each sex and 2 age classes (adult bears and subadults/yearlings) for each sex using all collared bears, but caution that age- and sex-specific estimates were likely affected by low sample sizes in some cases. In all survival models, we used 90% confidence intervals and set α to 0.1.

Cause-specific mortality

We used the non-parametric cumulative incidence function estimator (Heisey and Patterson 2006)—an extension of the Cox proportional hazards model—to estimate mortality risk from 2 causes of death: harvest and other. The "other" category included other human-caused deaths such as mortality due to motor vehicle accidents and natural deaths.

Covariates affecting mortality: GPS-collared bears. We used a stratified Cox proportional hazards model to test the effect of location (inside or outside

APP) and food availability on risk of mortality for GPS-collared black bears. Bear locations were marked as either "inside" (dummy coded 0) or "outside" (dummy coded 1) APP, and we created a new record in the survival table each time the bear moved inside or outside the park. We considered a day to be "inside" the park if $\geq$50% of the locations were inside the park. No mortalities occurred on days where bears crossed the park boundary. We assessed all models for the assumption of proportional hazards using the function cox.zph in the R package "survival"; we considered models acceptable if $P > 0.05$ (Therneau and Grambsch 2000).

We ranked annual fruit productivity for plant species eaten by black bears in APP qualitatively on a scale of 0-4, where 0 indicated no food productivity and 4 indicated a bumper crop (Potter et al. 2015). We averaged these values across species to obtain a mean food productivity value for each year inside APP. Dense red oak (*Quercus rubra*) stands are more common outside the park, and bears may leave the park to access acorn crops when the soft mast season is over. Therefore, we calculated the mean productivity score for the acorn crop each year for districts outside APP frequented by GPS-collared bears (Parry Sound and Bancroft districts). We coded food and oak as either low productivity (productivity <2.5) or high productivity (productivity $\geq$2.5) instead of assessing them as continuous variables to increase the number of samples in each category and facilitate interpretation of the results.

We assessed 6 Cox proportional hazards models with covariates for location inside or outside APP, food productivity inside APP, and acorn productivity outside APP. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989), modified to use the number of deaths as the sample size to rank models (Therneau and Grambsch 2000, Benson et al. 2014), and we computed sandwich standard errors by specifying a cluster term (Bear ID) in each model. We used a strata term to allow non-proportional hazards between deaths due to harvest and due to other causes. We report on models with $\Delta AIC_c < 2$. Although other covariates such as age, sex, whether involved in a human–bear conflict event, encumbrance, and year were of interest, our small sample size made it inappropriate to include more variables in the models. For example, the sample contained only 7 adult males (3 died), and deaths did not occur in all years of the study.

Covariates affecting mortality: VHF- and GPS-collared bears. We created a Cox proportional hazards model as above, but included only age class and sex as covariates in the model. We investigated whether sex primarily influenced probability of mortality for males and females due to harvest or other causes by coding 2 dummy variables as in Heisey and Patterson (2006), using code adapted for use in Program R and altering confidence intervals to 90% throughout the function. We report the number, location, and nature of all mortalities for collared black bears.

Results

Distribution of bears and bear harvest around Algonquin Provincial Park

Densities of resident black bears in WMUs within 53 km of the APP boundary (Tier 1) were significantly lower than in surrounding Tier 2 WMUs (Welch's $t = -2.58$, 12.2 df, $P = 0.012$; Fig. 2a). Natural-log-transformed percent projected harvest was much higher in WMUs near APP than in surrounding WMUs ($t = 2.18$, 16.3 df, $P = 0.022$; Fig. 2b). All Tier 1 WMUs had harvest rates >13% (Fig. 2b). Though percent projected harvest may appear high, raw harvest rates were similar. The highest projected harvest rates (51%, 109%, and 442% for WMUs 54, 75, and 55A, respectively; Fig. 2b) corresponded to high raw harvest rates (34%, 70%, and 354%, respectively). The percent projected harvest in WMU 55A was unusually high, possibly because of small sample sizes used in the population abundance estimate. When this WMU was excluded from the analysis, WMUs closer to APP still had higher percent projected harvest than surrounding WMUs ($t = 1.97$, 16.5 df, $P = 0.033$, Fig. 2b). Algonquin Park had higher resident bear density (31 bears/100 km^2) than all surrounding Tier 1 WMUs (1–22 bears/100 km^2; Fig. 2a).

Annual survival

There were 12 deaths for 31 black bears fitted with GPS collars in Algonquin Park, 2006–2014, and 21 deaths for the combined group of 72 VHF- and GPS-collared bears (Table 1; Fig. 3). Bears were harvested (only outside the park, $n = 7$ F, 7 M) or died inside the park, either of natural causes ($n = 3$ F), in a human–bear conflict event ($n = 3$ M), or in a motor vehicle accident ($n = 1$ F). Annual survival rate for all GPS-collared bears was 85.9%, 2006–2014 (90% CI = 79.9–92.3%; Fig. 4). For VHF- and GPS-collared bears combined, the annual survival rate was 85.1%, 2006–2014 (90% CI = 80.3–90.2%; Fig. 4). Adult male bears experienced much lower survival rates than females, whereas subadult and yearling survival was similar to that of adults (Table 2).

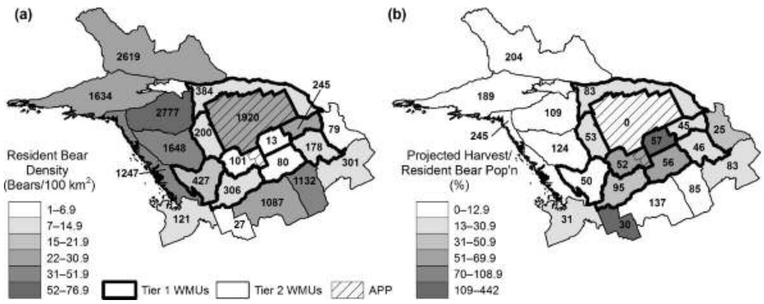

Fig. 2. Resident American black bear (*Ursus americanus*) density (a) and percent projected harvest (b) for bears in Wildlife Management Units (WMUs) in and around Algonquin Provincial Park (APP), Ontario, Canada, 2006–2014. In panel (a), shading indicates resident bear density (bears/100 km^2); labels on individual WMUs indicate the population size estimate. In panel (b), shading indicates projected harvest/resident bear population (%); labels indicate number of bears harvested (projected harvest).

Cause-specific mortality

For GPS-collared black bears, the annual mortality due to harvest was 9.1% (90% CI = 4.05–14.15%). The annual mortality due to other causes was 5.04% (90% CI = 1.63–8.44%). For VHF- and GPS-collared bears combined, the annual mortality due to harvest was 10.03% (90% CI = 5.85–14.21%), and for other causes was 4.9% (90% CI = 2.15–7.65%). Mortality due to harvest occurred mainly during the first week of the hunting season, whereas other mortality occurred more evenly throughout the season (Fig. 5).

Covariates affecting mortality: GPS-collared bears. The top model with $\Delta AIC_c < 2$ contained only the variable APP (Table 3). When black bears were outside APP, they were 7 times more likely to die than when inside the park (outside APP estimate = 1.94, Risk Ratio [RR] = 6.97, $P < 0.001$, 90% CI = 2.65–18.30). In the second- and third-ranked models (APP + overall food productivity and APP + oak productivity, respectively), bears were between 6 and 7 times more likely to die when outside APP (second-ranked model: [RR] = 6.32, $P = 0.008$, 90% CI = 2.00–19.92; third-ranked model: [RR] = 7.05, $P = 0.001$, 90% CI = 2.60–19.07). The risk ratios in these lower ranked models suggested the effects of food inside and outside the park were not significant in either model (second-ranked model: [RR] for decreased food inside park = 1.36, $P = 0.729$, 90% CI = 0.32–5.77; third-ranked model: [RR] for increased food outside park = 1.20, $P = 0.752$, 90% CI = 0.46–3.12).

Covariates affecting mortality: VHF- and GPS-collared bears. For VHF- and GPS-collared black bears combined, there was no significant influence of age class on risk of mortality (yearling estimate = −0.65, RR = 0.52, $P = 0.278$, 90% CI = 0.20–1.40; subadult estimate = −0.08, RR = 0.92, $P = 0.869$, 90% CI = 0.40–2.13). Adults and females were considered the reference classes. Males were >5 times more likely to die than females (male estimate = 1.72, RR = 5.57, $P < 0.001$, 90% CI = 2.58–12.03). When we coded 2 dummy variables to represent influence of sex on probability of mortality due to harvest or other causes, sex primarily influenced probability of harvest-related mortality (estimate = 1.84, RR = 6.32, $P = 0.001$, 90% CI = 2.63–15.18). In this analysis, the parameter estimates also suggested that males were >4 times more likely to suffer mortality from other factors compared with

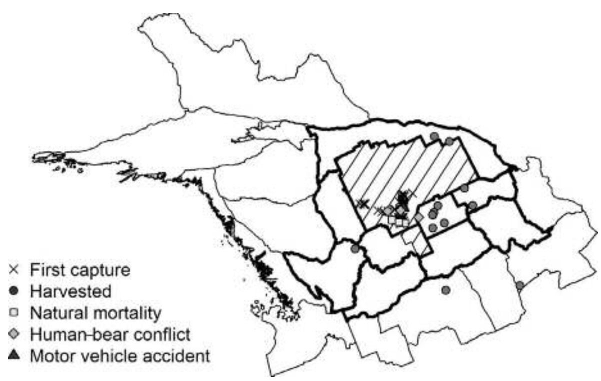

Fig. 3. Locations of first capture and deaths for 72 Very High Frequency– and Global Positioning System–collared American black bears (*Ursus americanus*) in Algonquin Provincial Park (APP; hatched), Ontario, Canada, 2006–2014.

Table 2. Annual survival estimates for American black bears (*Ursus americanus*) in Algonquin Park, Ontario, Canada, 2006–2014.

Sex and age class	Annual survival estimate (%)	90% CI	No. of individual bears	No. of bear-years[a]
Ad F	88.4	82.6–94.6	23	85
Subadult and yearling F	94.8	89.1–100.0	24	43
Ad M	63.2	40.8–98.1	7	9
Subadult and yearling M	60.0	43.3–83.2	26	28

[a]For example, a bear that wore a collar for 3 yr would equal 3 bear-years; all bear-years are summed to indicate the no. of years individuals were studied.

females (estimate = 1.45, RR = 4.28, $P = 0.090$, 90% CI = 1.04–17.56).

Discussion

We showed that densities of resident black bears were significantly lower in Tier 1 WMUs than in Tier 2 WMUs, and that percent projected harvest was much higher in Tier 1 WMUs than in Tier 2 WMUs. This, combined with higher resident bear density in APP compared with Tier 1 WMUs, strongly suggests that harvest in WMUs closer to the park is being subsidized, at least in part, by temporary emigration of APP resident bears to foraging areas outside the Park in late summer and autumn. Though it is possible that some subadult male bears may have left the park permanently, all monitored GPS-collared bears and most VHF-collared bears returned to the park each winter before denning, and we surmise that fidelity to general denning areas is strong. Harvest in Tier 1 WMUs also may be subsidized by temporary emigration of bears from Tier 2 WMUs. In Ontario, the recommended rate of human-caused mortality to maintain a black bear population is 10% in areas surrounding APP (Ontario Ministry of Natural Resources 2011); but we showed that harvest rates in Tier 1 occur at 13–442%. Though projected harvest may be slightly higher than real harvest, the majority (64%) of resident hunters reported on their harvest during the period of our study. Furthermore, non-resident harvest, which is reported very accurately (>95% reporting), made up almost one-third of the bear harvest in Tier 1 and 2 WMUs. Therefore, harvest in Tier 1 WMUs was clearly greater than can be sustained by the resident populations in those WMUs. Bears from APP appeared in the harvest and did not die of natural causes, and this could potentially threaten the ecological integrity of the Park via changes to the age and sex structure and abundance of the bear population. It is generally recognized that the age and sex structure of harvested bear populations differs from that of unharvested populations.

Annual survival of GPS-collared black bears in APP averaged 85.9%; and for all GPS-collared bears and VHF-collared bears combined, annual survival averaged 85.1%. Powell et al. (1996) studied survival of black bears in a system of reserves and surrounding hunted areas in North Carolina, USA, which was established so that the reserves would function as source populations

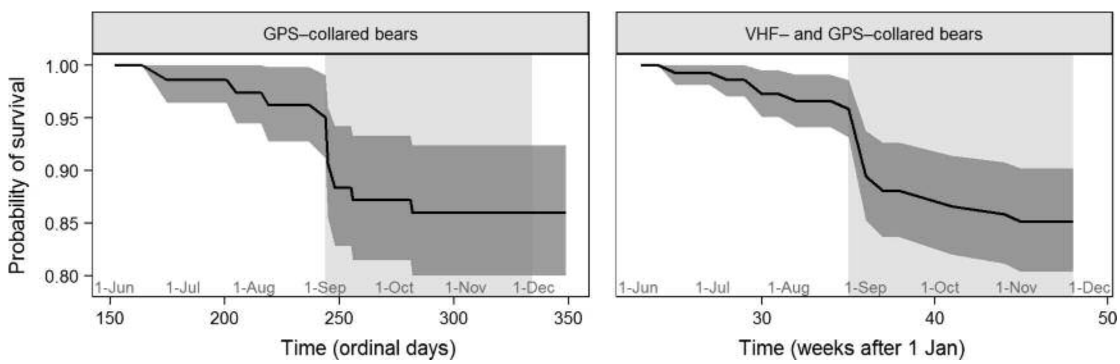

Fig. 4. Probability of survival and 90% confidence intervals (dark shading) of Very High Frequency (VHF) and Global Positioning System (GPS) -collared American black bears in Algonquin Provincial Park, Ontario, Canada, 2006–2014, showing the timing of hunting season (light shading).

Table 3. Models predicting mortality for 30 Global Positioning System–collared American black bears (*Ursus americanus*) in Algonquin Provincial Park (APP), Ontario, Canada, 2006–2014. k = number of parameters, LL = log likelihood, AIC$_c$ = Akaike's Information Criterion corrected for small sample sizes, w_i = Akaike weight.

Model	k	LL	AIC$_c$	ΔAIC$_c$	w_i
APP	1	−48.22	98.89	0.00	0.66
APP + Food	2	−48.15	101.80	2.91	0.15
Oak + APP	2	−48.18	101.86	2.97	0.15
Food	1	−51.6	105.65	6.76	0.02
Oak	1	−52.59	107.63	8.74	0.01
Oak + Food	2	−51.59	108.68	9.79	0.00

for the hunted areas. Specifically, they documented adult survival of only 76% in the Pisgah Bear Sanctuary and that density of bears inside the reserve was higher than outside, resulting in net emigration (Powell et al. 1996). As a result, Powell et al. (1996) concluded that the sanctuary functioned to provide dispersing bears for hunters and provided some protection for resident bears, but did not provide enough protection to ensure a viable breeding population within its boundaries. In contrast to APP, the Pisgah Bear Sanctuary is only approximately 400 km^2, much smaller than the 5,037-km^2 minimum area estimated by Gurd et al. (2001) necessary to avoid loss of mammals, so low survival rates of bears are not surprising.

Despite small sample sizes, survival of adult female black bears in our study (88.4%) may have been lower than that documented for adult females in the unhunted Chapleau Crown Game Preserve (CCGP) in Ontario's boreal forest (90.8%; Obbard and Howe 2008). The boreal forest is a region of the province where black bear population growth rate is expected to be lower than in the more productive mixed deciduous forests of central Ontario; therefore, it is surprising that adult female survival may have been lower in APP compared with rates in the CCGP. Average survival rate of yearling and subadult females in our study (94.8%) was considerably higher than rates reported for CCGP (approx.76%; Obbard and Howe 2008), but average survival of yearling and subadult males (60%) was lower than in CCGP (approx. 73%; Obbard and Howe 2008). Survival rates for adult males are not available for Ontario's boreal forest for comparison, and we acknowledge that the sample sizes of males in our study are small, which could introduce negative bias, especially when several males entered the study following a human–bear conflict. Nevertheless, the counterintuitively low average survival rates for subadult and adult males in our study compared with rates from the less productive boreal forest, and the slightly lower survival rates for adult females, raise questions about changes in age and sex structure and of sustainability of the APP black bear population.

In terms of cause-specific mortality, our study showed annual harvest mortality rate of GPS- and VHF-collared black bears combined averaged 10.0% and mortality due to other causes averaged 4.9%. In contrast, Obbard and Howe (2008) showed that harvest mortality averaged 3.2% in the boreal forest and other mortality averaged 6.0%. The higher mortality rate due to harvest for APP residents is of concern because Obbard and Howe (2008) concluded that harvest mortality was additive to other sources of mortality, rather than compensatory. In addition, we may have underestimated mortality rates for subadult bears fitted with VHF radiocollars. Budgetary constraints meant we could not fly frequently enough to thoroughly monitor dispersing males; therefore, we lost

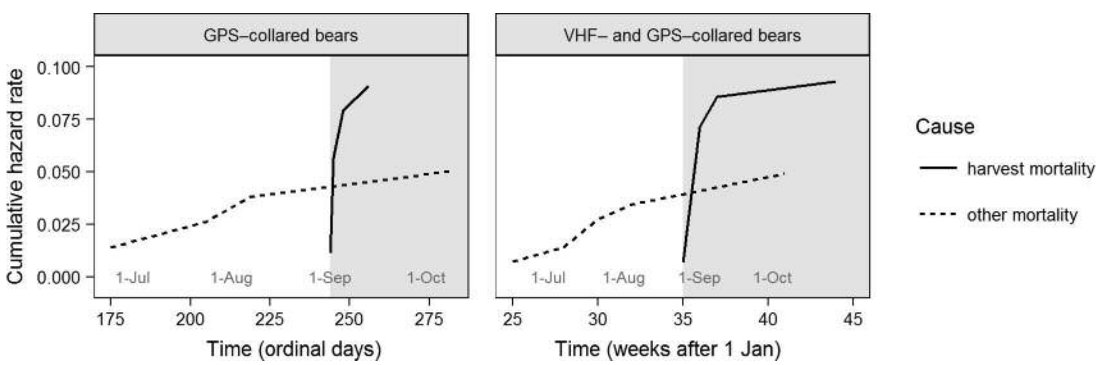

Fig. 5. Cumulative hazard rate for harvest-related and other causes of mortality for Very High Frequency (VHF) and Global Positioning System (GPS) -collared American black bears (*Ursus americanus*) in Algonquin Provincial Park, Ontario, Canada, 2006–2014, showing the timing of hunting season (light shading).

contact with some dispersing males and censored them from the data set before their ultimate fates could be determined.

Cause-specific survival estimates for GPS-collared black bears and VHF- and GPS-collared black bears combined were similar. Although we assumed that most harvest-related deaths were known for all studied bears because all GPS-collared bears that were harvested were reported to us by the hunter or outfitter, we acknowledge that deaths due to natural causes were likely slightly under-represented for VHF-collared bears. Therefore, overall survival was likely over-estimated and mortality estimates due to harvest are likely more reliable than mortality estimates due to "other" causes of death.

We acknowledge that harvest-related mortality for collared black bears may be biased. First, hunters may have avoided killing collared bears, though some hunters clearly did not do so. Our overall study had several objectives, including monitoring seasonal movements and describing habitat use during late-summer forays. Therefore, in the first 3 years of the study, prior to the opening of the autumn bear-hunting season, we sent a letter to local outfitters reminding them of the study and requesting that they advise their clients to avoid harvesting radiocollared bears. We recognize that this may have resulted in an under-estimate of hunting mortality; however, there is no way to know whether hunters passed up an opportunity to harvest a radiocollared bear. Second, some bears ($n = 9$) were radiocollared and entered into the study because they were involved in human–bear conflict at campsites in APP and were likely human-habituated and food-conditioned. These bears were more likely to be dispatched if they were involved in repeat conflicts. Additionally, because hunting over bait is the predominant method used in Ontario, especially by non-resident hunters (de Almeida and Obbard 2005), these bears may have been more vulnerable to harvest, which might have contributed to an over-estimate of hunting mortality. Nevertheless, our study was intended to investigate all causes of mortality of bears in APP, so including the fate of such habituated bears was appropriate.

We showed that black bears were 7 times more likely to die when outside APP. Although risk of mortality tended to increase both when there was overall lower food availability inside APP or when oak was abundant outside APP, the increases were not statistically significant. Our ability to detect a significant effect of low food abundance on risk of mortality may have been hampered by small sample sizes in some years. In the boreal forest of Ontario, resident bears of CCGP also were vulnerable to harvest when on late-summer forays outside the preserve, but the greatest increase in mortality risk was when adult females were encumbered with cubs (Obbard and Howe 2008). Adult females were twice as likely to die from all causes (though no more or less likely to be harvested) and nearly 10 times as likely to be cannibalized when encumbered with cubs. This was especially notable in the second year after a year of widespread food failure when most adult females in the study population (both inside and outside the game preserve) were encumbered with cubs (Obbard and Howe 2008). So, the delayed effect of low food availability on mortality rates may be higher in the boreal forest than in the Great Lakes–St. Lawrence forest, which has a greater diversity of potential forage species for black bears. This greater diversity may act to reduce the impact of loss of any one food species and dampen variability in mortality rates.

The American black bear is a habitat generalist and, as a large carnivore with a large home range, it can be considered a classic umbrella species (Wilcox 1984, Shafer 1995). Black bears perform important roles in ecosystem function, such as seed dispersal (Rogers and Applegate 1983, Enders and Vander Wall 2012). Therefore, providing protection for black bears, including protection of habitat, should benefit a wide range of other species and help ensure a properly functioning ecosystem. However, similar to the system studied by Powell et al. (1996), we showed that the largest protected area in southern Ontario (Algonquin Provincial Park) does not provide complete protection for its resident bears, especially for any with home ranges within 20 km of a park boundary. This is a challenge for Park managers who are charged with maintaining the ecological integrity of the Park because a proportion of Algonquin Park's bears are subjected to sources of mortality that are not characteristic of the natural region (i.e., where only natural mortality would occur) and are clearly changed by human activity outside the Park's boundary. In response to a similar threat to the viability of Algonquin Park's wolves, an issue raised in the 1990s (Theberge and Theberge 1998), harvest of wolves was prohibited in those townships surrounding the Park in 2001 (Government of Ontario 2001). The other challenge for Park managers, and indeed other wildlife managers in the region, is that the high harvest levels in townships surrounding Algonquin appear to be subsidized, at least in part, by Park bears on seasonal forays. This contradicts the charge given to park managers to maintain ecological integrity as defined under Ontario's *Provincial Parks and Conservation Reserves Act, 2006.*

Recently, in a study of protected areas worldwide, Gray et al. (2016) showed that biodiversity in terms of species richness and abundance were 10.6% and 14.5% higher, respectively, inside protected areas than outside these same areas. Currently, this finding applies to black bears in APP because abundance of black bears inside APP is higher than in areas immediately adjacent to the Park (though the low density immediately adjacent to APP is almost certainly due to high harvest levels). Nevertheless, the low survival rate of males in our study suggests that the situation warrants continued monitoring.

If parks or other protected areas are intended to act as natural points of reference to support monitoring of ecological change or maintain ecological integrity, a landscape approach to managing black bear populations should be considered where source–sink conditions exist. Where hunted areas border protected areas, managers should identify the origin of harvested bears in order to ensure that ecological integrity of the protected area is not compromised even if the protected area was established originally to provide a source population to subsidize harvest (sensu Powell et al. 1996).

Management implications

Algonquin Provincial Park is a large protected area compared with most of those in North America and elsewhere. Therefore, our results should serve as a cautionary tale to managers charged with ensuring viability of bears in a landscape where the protected area is an island surrounded by areas of high human disturbance. Individuals of many bear species around the world are killed when they come into conflict with humans (e.g., farmers, residents of villages and towns, hunters, poachers) outside protected areas. Managers should be cautious about assuming that parks or preserves provide adequate protection for resident bears against population decline without a thorough analysis of movement patterns, mortality data, and changes in age and sex structure.

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