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Male elk survival, vulnerability, and antler size in a transboundary and partially migratory population

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Abstract

Migration is a behavioral strategy used by many ungulates to access resources and avoid predation in heterogenous landscapes. If migratory individuals access higher quality forage and avoid predation, then they should attain greater fitness. Migration can also expose individuals following distinct migratory tactics to differential mortality and harvest. We investigated how transboundary migration affected male elk (Cervus canadensis) survival and antler size when subjected to harvest with different antler point restrictions (APRs) and yearround harvest by treaty First Nations in a multi-carnivore system in Alberta, Canada. We measured antler size and age for 35 unmarked, harvested male elk and 90 global positioning system (GPS)-collared adult male elk. We also estimated radiocollared elk survival and cause-specific mortality (105 elkyears) from 2018 to 2020. Antler size increased as a non-linear function of age and exposure to high quality forage for migrants. The biological effect size of exposure to higher quality forage (i.e., lower biomass) obtained by migrants was variable but biologically equivalent to the antler size difference (i.e., 33–54 cm) predicted between 5- and 6-year-old male elk. Annual mortality rate was 0.304 and the primary cause of death was hunting (cumulative incidence functions [CIF] mortality rate = 0.203, n = 33 mortalities) of which a third was by First Nations treaty harvest (CIF = 0.101, n = 12).

J Wildl Manag. 2023;87:e22386. wileyonlinelibrary.com/journal/jwmg 1 of 22

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Non-human-caused mortality was rare (CIF = 0.015); only 2 males died because of predation by wolves (Canis lupus). Sixpoint APRs resulted in lower annual survival rates (S = 0.42) for male elk with ≥6 antler points, which were usually >4 years of age. Harvest risk increased by 20% for every 1-km closer to an access road. Elk harvested by licensed recreational or First Nations hunters were similar with respect to male elk age, antler size, date, and location. There was very little evidence that multiple species of large carnivores influenced male elk survival. These results indicate forage quality and vulnerability to harvest by humans influence male elk age structure, and hence antler size, of transboundary and partially migratory populations, even in carnivore-rich complex systems.

KEYWORDS

antler point restriction, antler size, Banff National Park, Cervus canadensis, forage quality, harvest, hunting, male elk, migration, ungulate

In many harvested ungulate populations in western North America, males are harvested disproportionally to females. This is because of the weaker effect of male harvest on population growth rate (hence managers often consider their harvest a surplus), except when extreme levels of harvest result in extremely low male:female ratios (Hines et al. 1985, Mysterud et al. 2002). Male ungulates with larger antlers or horns are also often held in high esteem by hunting cultures in western civilization because of their aesthetic trophy quality (Monteith et al. 2013). Definitions of trophy animals vary and are ultimately arbitrary but are more objectively described by antler (or horn) size. The most important factor increasing antler (and horn) size in ungulates is survival to older ages (Wolfe 1982, Hewitt et al. 2014, Jones et al. 2018). Improved nutrition also enhances antler growth, and quantitative genetic studies demonstrate a small but important role of heritability in explaining antler size (Strickland et al. 2001, Kruuk et al. 2002, Jones et al. 2018). Recreational harvest is often the main cause of mortality for adult males in hunted populations (Keller et al. 2015). Hunting regulations, hunter accessibility, and selectivity for larger antler and horn sizes are thus the primary factors influencing male ungulate survival and antler size in harvested populations (Unsworth et al. 1993, Cole et al. 1997, Hayes et al. 2002).

Wildlife and land managers commonly use 4 strategies to regulate ungulate harvest including timing the hunting seasons outside the breeding season, limiting the number of hunters, constraining hunter's access by limiting road density and closing roads, and, for harvest of males, implementing antler-point (or horn-length) restrictions (APRs) that allow escapement of younger or older age classes (Stalling et al. 2002). Objectives for male harvest vary from maximizing harvest numbers (open hunting seasons with no restrictions), encouraging harvest on young males instead of mature males (e.g., spike yearling male elk), emulating natural age structures of males, meeting minimum male:female ratios after the harvest to promote successful reproduction (Noyes et al. 1996), or managing for maximum antler size (e.g., trophy) males. Wildlife managers frequently rely on APRs to obtain an older age structure and more large-antlered males; however, the effectiveness of APRs in increasing the antler size of harvested individuals is unclear. There is conflicting evidence that APRs allow individuals to reach advanced ages and maximize their antler size (Wolfe 1985, Bender and Miller 1999, Biederbeck et al. 2001). Instead, APRs are most successful in limiting the harvest of younger age classes and increasing the male:female ratio (Wolfe 1985).

Regardless, there are fewer studies on the effects of harvest regulations and their effect on male elk (Cervus canadensis) survival, especially in systems with abundant large carnivores.

Predation by carnivores can affect male survival and thus age-dependent traits of ungulates such as antler size and body mass (Metz et al. 2018). Elk occur across North America and play an important ecological role as large herbivores, provide hunters opportunities for recreational and subsistence harvest, and are a primary food source for large carnivores (Metz et al. 2012, United States Census Bureau 2016). The recovery of large carnivores through recolonization and reintroductions across western North America has altered the predation landscape for elk (Varley and Boyce 2006, Brodie et al. 2013). Studies have since shown gray wolf (Canis lupus) predation can be the leading cause of mortality for female elk (Brodie et al. 2013, Hebblewhite et al. 2018). Wolves in Yellowstone National Park selected for older males (hence, with larger antlers) in early winter following the rut when they were in poor condition (Winnie and Creel 2007, Metz et al. 2012). Thus, wolf predation potentially could reduce male elk survival, abundance, harvest, and antler size, a controversial management concern. Most of the few studies on male elk survival and antler size are from the 1990s and early 2000s in areas where wolves and other large carnivores were absent (Unsworth et al. 1993, Hayes et al. 2002, McCorquodale et al. 2003). Thus, there have been few studies on the effect of predation on male elk survival, and hence antler size, in such carnivore-rich landscapes.

Migration can also affect survival, antler size, and harvest of male elk (Boyce 1991). Most ungulate populations are partially migratory, where some migrate and some remain resident year round (Berg et al. 2019). Partial migration can often create spatiotemporal variation in exposure to harvest that may differentially affect migratory tactics (Sawyer et al. 2016). This is common when there is a mixture of public and protected (private) lands with variation in harvest pressure (Boyce 1991, Smith 2007, Proffitt et al. 2013). Many elk populations move into national parks (e.g., Yellowstone, Rocky Mountain, Grand Teton, and Banff national parks) where they are protected, creating transboundary refugia from hunting (Hebblewhite 2006, Loe et al. 2016, Meisingset et al. 2018). Spatial vulnerability to harvest is also affected by the timing of migration where males often migrate from public lands where they are vulnerable to harvest to protected area refugia or vice versa (Boyce 1991, Smith 2007, Proffitt et al. 2013). Harvest of individuals in a partially migratory population may depend on whether males are resident or migratory (Rivrud et al. 2015, Hebblewhite et al. 2018), with important implications for male survival and age structure, and hence antler size. Migratory ungulates also often have access to higher forage quality than residents, which can increase female body condition, pregnancy rates, calf masses, and survival (e.g., the forage maturation hypothesis; Hebblewhite et al. 2008), and reduce exposure to predation. There have been fewer tests of predictions of the forage maturation hypothesis that migratory males will have larger antlers, however. The Ya Ha Tinda elk population in and adjacent to Banff National Park, Alberta, Canada (Hebblewhite et al. 2006) has amongst the highest large-carnivore mortality rates on adult female elk and neonates in North America (Brodie et al. 2013, Berg et al. 2023), with abundance limited by wolf and grizzly bear (Ursus arctos horribilis) predation (Hebblewhite et al. 2018). Yet it is also one of Canada's premier trophy male elk hunting areas, with some of the largest trophy size male elk harvested in Canada. Understanding the drivers of male elk survival in this system would provide managers valuable insight into these questions in similar systems across western North America.

Our research objective was to investigate the potential drivers of male elk survival and antler size in this transboundary, partially migratory population of elk. We tested for the effect of migratory tactic (migrant, resident) and exposure to forage quality on antler size. We predicted that migratory males, like females (Hebblewhite et al. 2008), would be exposed to higher forage quality, and would have larger antler size than residents. The forage maturation hypothesis also predicts that starvation-related mortality, but not other causes, should be higher for residents. Thus, we tested if cause-specific mortality differed by migratory status. Previous studies have also shown that wolf predation was a key cause of winter mortality especially after the rut when males were in poor condition (Metz et al. 2012). We predicted that winter wolf predation would be greater for resident elk because exposure to lower forage quality (Hebblewhite et al. 2008) would leave them in poorer condition than migrants. We tested for spatiotemporal harvest factors that might differentially affect migrant and resident male survival including access to protected national parks, exposure to different APRs, and exposure to road networks. We predicted elk that spent more time in Banff National Park (i.e., no hunting) would experience higher survival (Anderson 1958, Rudd et al. 1983), whereas older-aged male elk subject to APR harvest would have lower survival than younger-aged male elk. Lastly, we predicted male elk survival would be lower when using areas closer to roads (Unsworth et al. 1993, Ranglack et al. 2017).

STUDY AREA

We studied theYa HaTinda elk population from 2017 to 2020 and defined the study area as the annual range of theYa HaTinda elk population (51°30′N, 115°30′W; Figure 1), a 7,000-km^2 area on the eastern slopes of the Canadian Rockies in and adjacent to Banff National Park (BNP) and eastern foothills of Alberta, Canada (Hebblewhite et al. 2006). Vegetation falls into 3 ecoregions and follows a west–east elevational gradient (3,600–1,600 m), from alpine and subalpine summer ranges in the west to montane foothills in the east. Vegetation in the montane ecoregion consists of lodgepole pine (Pinus contorta) and Engelman spruce (Picea engelmannii), interspersed with willow (Salix spp.) riparian areas, aspen (Populus tremuloides) parklands, and grasslands. At higher elevations in the subalpine and alpine ecoregions, the Engelmann spruce and lodgepole pine forests include subalpine fir (Abies lasiocarps) and riparian areas consist of willow–shrub communities. Subalpine grasslands and shrub-forb meadows are common in the alpine ecoregion. The climate is cold continental with long, snowy winters (Oct–Apr) and a short growing season between June and August. The primary winter range is centered on the privately owned 3,945-ha Parks Canada Ya Ha Tinda Ranch (Figure 1) and is composed of a 20-km^2 rough fescue (Festuca campestris) grassland in the province of Alberta and is the namesake of the region Ya Ha Tinda, which means mountain prairie in the Stoney-Sioux language.

Elk were the most abundant ungulate in the study area with an estimated population size of about 500 animals (Martin et al. 2022) after a decline due to predation from a peak of 2,200 elk in the late 1990s (Hebblewhite et al. 2006, 2018). Other ungulates include, in approximate order of abundance, bighorn sheep (Ovis canadensis), mule deer (Odocoileus hemionus), white-tailed deer (O. virginianus), moose (Alces alces), and mountain goats (Oreamnos americanus). Wolf predation is the leading cause of adult female elk mortality, but humans, grizzly bears, American black bears (U. americanus), cougars (Puma concolor), and coyotes (Canis latrans) also kill adults and neonates

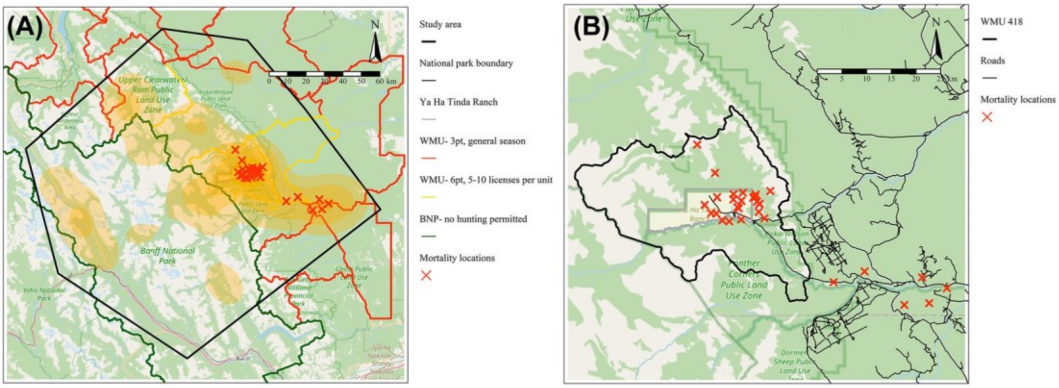

FIGURE 1 A) TheYa HaTinda study area located in and adjacent to Banff National Park (BNP; outlined in green) in Alberta, Canada, with 95% isopleths of kernel density (yellow shading) for radio-collared male elk during September 2018–2020, with mortality locations delineated by red ×s. Mountain wildlife management units (WMU) with a 6-point (6 pt) antler point restriction (APR) and special licenses are outlined in yellow, and foothill WMUs with 3-point APR (3 pt) and general licenses

are outlined in red. Banff National Park does not allow hunting. B) Wildlife management unit 418 in Alberta, Canada, with roads and mortality locations of harvested male elk with known mortality locations, 2018–2020.

TABLE 1 Wildlife management units (WMUs) and corresponding male elk tag allocations and antler point regulations (APR) for WMUs that represent harvest exposure of the Ya Ha Tinda elk population in Alberta, Canada, 2017–2020.

Region	WMUs	APR	Archery season	Rifle season	General licenses	Outfitter licenses
Foothills	314, 316, 318, 320	3-point	1 Sep–30 Oct 1 Sep–24 Oct (WMU 314)	1–30 Nov 25 Oct–30 Nov (WMU 314)	Unrestricted	0
Mountain	414, 416, 417, 418, 420, 422	6-point	25 Aug–16 Sep	17 Sep–1 Nov	30	9
Minister's Special License	Any WMU		Defined by WMU	Defined by WMU	0	2

(Hebblewhite et al. 2018, Berg et al. 2023). The Ya Ha Tinda elk population is partially migratory with 3 migratory tactics characterized by differences in survival and choice of summer range: eastern migrants, western migrants, and residents (Berg 2019, Martin et al. 2022). Male and female migrants begin migration in May or June, returning to winter ranges from September–November, whereas the residents remain year-round on the winter range centered on the Ya Ha Tinda Ranch (Hebblewhite et al. 2006, Martin 2021).

Hunting occurs only on provincial portions of the study area (Figure 1) where Alberta Environment and Parks manage hunting regulations within wildlife management units (WMUs). Wildlife management unit 418 includes the elk winter range and the Ya Ha Tinda Ranch (Figure 1B). Summer ranges span multiple WMUs including the foothills of WMUs 314, 316, 318, and 320 (where eastern migrants summer), which have 3-point APRs (minimum of 3 antler points on 1 side), and the mountain region (where western migrants summer), consisting of WMUs 414, 416, 417, 418, 420, and 422, which have 6-point APRs (minimum of 6 antler points on 1 side; Figure 1; Table 1). There has not been any licensed female harvest in this region since the early 2000s, though treaty First Nations harvest of females and males legally occurs year-round, though it is concentrated in the fall (Hebblewhite et al. 2018). Six-point restrictions are often used in Alberta to maximize quality and quantity of male elk harvest (i.e., the greatest number of ≥6-point males), whereas 3-point APRs are used to maximize overall male harvest. Timing of hunting seasons vary by WMU, but usually archery seasons start in early September and rifle seasons begin between 17 September and 1 November (Table 1). Thus, there are 41 licenses potentially available across all combined mountain WMUs. In the 1990s, Alberta Environment and Parks implemented a wildlife road sanctuary that prohibits hunting within 365 m of the main road used to access WMU 418 and runs along the southern boundary of WMU 417 and northern boundary of WMU 416. In addition to recreational hunting managed by Alberta Environment and Parks, treaty First Nations can legally harvest elk year-round on land where they have the right of access (e.g., crown land) or permission to hunt but are still subject to the road hunting sanctuary regulation. There is currently no First Nations hunting permitted in Banff National Park, but Parks Canada does permit hunting by First Nations and licensed hunters on the privately owned Ya Ha Tinda Ranch.

METHODS

We used data from radio-collared and hunter-harvested male elk to investigate factors affecting survival and antler size. We used antler measurements collected on captured and hunter-harvested males. We monitored movements of global positioning system (GPS)-collared males to determine migratory tactic, monitor exposure to forage quality, and estimate survival. We first modeled the effects of age, migratory behavior, and forage quality on antler size of both GPS-collared and harvested male elk. Because males shed and re-grow (usually larger) antlers as they age, we used the relationship between antler size and age from captured male elk in January to predict antler sizes of radio-collared male elk in the following fall seasons to assess the effect of antler size on subsequent survival. Next, we assessed the risk of mortality of different age classes to recreational harvest based on the proportion of legal males (>6 points on 1 antler). Finally, we estimated male Kaplan-Meier survival rates, the effects of spatiotemporal factors influencing survival using Cox proportional hazards models, and cause-specific mortality using cumulative incidence functions (CIF; Heisey and Patterson 2006).

Antler size and migratory classification

We captured and radio-collared male elk each January of 2018, 2019, and 2020 when they had antlers. We used aerial (n = 79) and ground darting (n = 3) with butorphanol tartrate, azaperone tartrate, and medetomidine hydrochloride (BAM; Wolfe et al. 2014) to safely capture 32, 29, and 21 branch-antlered males in each year, respectively. We fit male elk with Vectronics Survey Iridium (VECTRONIC Aerospace GmbH, Berlin, Germany) or Lotek LifeCycle Globalstar (Lotek Wireless, Newmarket, Ontario, Canada) GPS-collars that collected a GPS location every 13 hours, detected and reported mortalities after 6 hours of inactivity, and transmitted GPS locations (and mortality events) via Iridium or Globalstar satellite transmission. To allow for neck expansion during the rut, we tested 13 collars with magnetic expansion strips (LOTEK, Newmarket, Ontario, Canada) in 2018. All collars also had drop-off mechanisms and were fit loosely with a foam liner that allowed for neck expansion. We ear-tagged radiocollared males with a unique ID using a Ketchum ear tag (Ketchum Manufacturing, Tamperproof Ear Tags, Lake Luzerne, NY, USA) and an Allflex sheep ear tag (Allflex Livestock Intelligence, Dallas, TX, USA) with project contact information. Tags were also inscribed with ‘Do Not Eat Before Calling’ to prevent people from consuming animals before the recommended veterinary withdrawal time of BAM. We extracted a vestigial canine and submitted teeth to Matson's Laboratories (Manhattan, MT, USA) for histological aging (i.e., known-aged) using cementum annuli analysis (Hamlin et al. 2000). Trained personnel determined cause of death as soon as a mortality was detected (usually within 1–3 days) using evidence-based criteria in the field (Alt and Eckert 2017).

Personnel trained to use the Safari Club International's (SCI) scoring system measured the antlers of captured, hunter-harvested, and opportunistically found dead male elk. The SCI scoring system measures the cumulative antler beam length (in inches), tine length, distance between the antler beams, and circumference at base of beam (Schwabland et al. 2019), and hereafter is referred to as antler size. Hunters and outfitters who had been sent forms and instructions on how to measure the antlers also collected antler measurements from harvested elk if research personnel were not present to measure antlers.

We classified the migratory status of adult males in each year using non-linear modeling of net-squared displacement following Bunnefeld et al. (2010). We used the MigrateR package (Spitz et al. 2017) in program R (R Core Team 2017) to define migratory tactic and verified each classification visually following Eggeman et al. (2016). We classified male elk as western migrants when they migrated west into Banff National Park, or eastern migrants for those migrating east into the foothills (Figure 1; Martin et al. 2022). Following Eggeman et al. (2016), we classified male elk that remained within 15 km of the winter range year-round (i.e., maximum range of exploratory movements) as resident. Despite frequent switching of migratory tactics by female elk in this population (15%/year; Eggeman et al. 2016), there was limited switching in males (n = 2). Therefore, we assumed the migratory tactic for captured male elk in biological year t − 1 was the same in biological year t once they were collared.

Antler size analysis

To test for the effects of forage on antler growth, we used values of forage biomass (g/m^2) and its inverse relationship with forage quality from a previously developed landscape nutrition model. Hebblewhite et al. (2008) developed an empirical landscape nutrition model predicting peak-growing-season (~4 Aug) forage biomass (g/m^2) from approximately 1,000 vegetation plots and spatiotemporal covariates such as land cover type, slope, aspect, elevation, and time-varying normalized difference vegetation index (Hebblewhite et al. 2008). Peak season biomass estimates were updated annually to account for changes in land cover and successional change in burns and clearcuts (Berg et al. 2021). Because elk diet consists primarily of forbs and graminoids during the summer period of antler growth (Hebblewhite et al. 2008), estimates included only herbaceous biomass (forbs plus graminoids). Moreover, because Hebblewhite et al. (2008:Figure 5) showed that forage quality (dry matter digestibility [% DMD]) was inversely correlated with forage biomass in our study area, we interpret high forage biomass as low forage quality following the forage maturation hypothesis (Fryxell 1991). This forage biomass-quality model was demonstrated to predict higher fecal nitrogen for elk who spent time in higher forage quality areas, and higher pregnancy rates, mid-winter calf masses, and calf survival, confirming the real benefits of migration in our system (Hebblewhite et al. 2018, Martin et al. 2022). We extracted peak of forage biomass values (mean predicted biomass in Aug) at all summer (1 Jun–31 Aug) GPS-collar locations when individual males were on the summer range and thus growing antlers. We centered peak herbaceous forage estimates on the mean value of herbaceous biomass ($\bar{x}$ = 42.8 g/m^2) and scaled values by dividing by 1 standard deviation of the mean (SD = 14.07).

We developed a suite of generalized linear mixed-effect models (GLMM) to assess the effects of age, migratory status, and forage biomass on male elk antler size from captured males in January of year t. We modeled antler size in inches, not metric cm, because most North American trophy measurement systems are in inches. We considered 3 sets of models to address different but interrelated questions with slightly different subsets of data. We first developed a model for the relationship between antler size (y) and elk age (x) of known age males captured in January or harvested in the subsequent fall (n = 90). Because antler size often peaks at 7–10 years of age once body mass is reached (Wolfe 1982, Bender et al. 2003, Hewitt et al. 2014), it is typically described by an asymptotic growth equation (Kruuk et al. 2002, Bender et al. 2003). But we did not observe any individuals >6 years old that may have reached asymptotic antler growth. Nonetheless, we used model selection to compare linear, non-linear quadratic, and categorical age (1–3, 4, ≥5 yr) models for best fit. We defined 3 age classes (1–3, 4, and ≥5 yr) to account for the differences in the proportion of legal males (under the 6-point APR) in each age class (Table 2). We used the best fit antler size age model in all subsequent models.

Second, we assessed the effect of migratory tactic and biological year on antler size using elk of known age and migratory tactics. Because some elk captured in January died or experienced collar failure before migration, the sample sizes for this second set of models was reduced compared to our first analysis (n = 86). We included migratory tactic as migrant or resident categories as a proxy for exposure to the benefits of migration, which

TABLE 2 The proportion of radio-collared male elk in each age class that were not legal under the 6-point antler-point restriction, were legal but only had 6 legal points on one antler, and were legal with 6 legal points on both antlers, and mean Safari Club International (SCI) gross score (antler size, in inches) in the Ya Ha Tinda population, in and adjacent to Banff National Park, Alberta, Canada 2017–2020.

	<6 points (not legal)		6 legal points on 1 side		6 legal points on both sides		SCI gross score	
Age	n	%	n	%	n	%	$\bar{x}$	SD
1	1	100	0	0	0	0	169.8	
2	30	91	2	6	1	3	171.1	39.65
3	22	76	1	3	6	21	216.5	33.53
4	5	36	3	21	6	43	263.3	33.39
5	2	25	3	38	3	38	273.1	36.99
6	0	0	2	50	2	50	316.9	27.95

included enhanced forage or reduced risk of predation and harvest. We also included biological year as a fixed effect to control for weather conditions known to influence early antler and horn growth (Smith 1998, Schmidt et al. 2001).

In our third and final GLMM, we used the smallest subset of GPS-collared male elk (n = 22) for which we also had GPS location data corresponding to the summer growing period (Jun–Aug) prior to antler measurement to explicitly test for the effects of exposure to forage biomass on antler size. We then explicitly tested for the effect of summer exposure to forage biomass at GPS locations of male elk (13-hour fix rate).

For all GLMMs, we used a Gaussian (normal) link function for antler size because it was normally distributed and included a random effect for individual elk to account for repeat antler measurements over time (n = 25). We used the lme4 package (Bates et al. 2015). We used Bayesian Information Criterion (BIC) to rank the models because the stiffer penalty in BIC guards against overfitting compared to Akaike's Information Criterion (Neath and Cavanaugh 2012). We report the beta coefficients for the top models without model averaging.

Adult male survival

We derived annual non-parametric Kaplan-Meier survival estimates, and then tested for factors (age, migratory tactic) affecting survival during just the hunting season using Cox proportional hazards models. We right censored males if they dropped their collar or collars failed and interval censored males if the collar did not send a fix for >30 days (DeCesare et al. 2016). We used a recurrent biological year origin date of 1 June because the migratory tactic of an individual was usually known on 1 June and the birth pulse occurred on 1 June (Fieberg and DelGiudice 2009). We estimated annual Kaplan-Meier survival (Hosmer et al. 2011) of adult males over 2.5 biological years (1 Jun 2018–1 Dec 2020). We tested categorical differences in annual survival between age classes (2–3, 4, ≥5 yr) and migratory tactic using a log-rank test in the program R package survival (Therneau and Grambsch 2000). Age classes for survival models were different than antler size models because we only tested for factors affecting survival in the fall hunting season when males that were 1.5 years old in January captures were ≥2 years old.

We determined factors affecting survival during the hunting season (1 Sep–30 Nov) in a time-to-event framework with fixed- and time-varying covariates, a daily survival interval (Fieberg and DelGiudice 2009), and a staggered entry design with right, left, and interval censoring (Andersen and Gill 1982, Hosmer et al. 2011). We focused on only the hunting season because few mortalities occurred outside this period, and to focus on factors affecting vulnerability to harvest. Also, no non-hunting mortalities occurred during this hunting season. We developed models to test the effect of the 3 age classes (2-3, 4, ≥5 yr), predicted antler size, distance to road, migratory tactic, inside and outside Banff National Park, and hunting regulation (6 APR, 3 APR) on male elk survival during the hunting season. We predicted antler size for males during the fall harvest using our top model for antler size of radio-collared males the year prior to harvest. We first fit the antler size GLMM model to measured antler size in January, and then created a new data set that forecasted the age of the collared animal to the end of the study. Then, we used the predict interval function in the merTools R package to predict the median (50th percentile) antler size from when the elk was first captured to the end of the study (Knowles et al. 2020). We ignored prediction error for antler size, which likely led to our underestimating uncertainty of the effect of antler size on survival. We then used predicted antler size in Cox models. We did not use male elk age and predicted antler size in the same model because antler size was predicted as a function of age. We also did not include migratory tactic and distance to road because they were strongly correlated. We present the results of age and predicted antler size elsewhere (Martin 2021) to be able to be compare across studies and for potential later use in age-structured matrix population models.

We used the Alberta road layer (Alberta Environment and Parks 2020) to calculate the distance (km) of elk GPS locations during the hunting season and mortality sites to roads (unimproved, logging road, or truck-trail). We grouped all types of roads because of the modest number of mortalities, and because all roads could be accessed via off-road vehicles and provide hunter access. We recorded distance to the closest road for the daily survival interval because GPS locations were recorded every 13 hours. For individuals that had unknown mortality locations, we calculated the mean distance to the nearest road from the previous 3 days and used that as a distance metric for the mortality location (Johnson et al. 2004). We tested for differences in characteristics of First Nations and recreational harvest within WMU 418, where most of the harvest occurred. We tested for differences in the age, antler size, distance to road, and ordinal date between First Nations and recreational harvest using a Welch t-test.

We categorized the causes of mortality as wolf, recreational harvest, First Nations harvest, grizzly bear, starvation, or unknown (non-predator). We estimated cause-specific mortality of radio-collared male elk using CIFs from 2018 to 2020 (Heisey and Patterson 2006). We categorized harvest (and wounding loss) as recreational or First Nations harvest depending on the timing of the harvest relative to recreational season dates, and by direct communications with hunters in the field when we retrieved collars. Cumulative incidence functions account for competing risks and the number of individuals at risk to estimate the probability of mortality (i.e., mortality rate) from a given cause (Heisey and Patterson 2006). We then tested for differences in CIFs between migratory tactics and years using Gray's test in the cmprsk R package (Gray 1988, 2020; Pintilie 2006). Because harvest (First Nations and recreational hunters) was the overwhelming cause of mortality, we did not examine temporal or spatial differences among causes.

RESULTS

We captured and radio-collared 75 unique male elk in 82 capture events (7 recaptures) and monitored these elk for 107 elk-years. Of the 75 unique males, 40 radio-collared males died, but 2 were censored because of collar failure prior to harvest and 2 additional males died and were censored when their antlers became entangled in each other's collars. This resulted in 36 mortalities used in the analysis. Nine of 13 collars with magnetic expansion strips broke off within the first 16 months of deployment, and were thus right censored, and the remaining 4 elk were harvested within 10 months of deployments. Seven radio-collars with timer or remote drop-offs released prematurely and thus were also right censored. We observed no morbidity or mortality due to neck choking from the fixed-length collars, nor did we find evidence of collar fit being too tight when we recaptured males, checked hunter-harvested males, or observed males in the field using spotting scopes or remote cameras.

We classified migratory behavior for each of 107 radio-collared elk-years. Western migrants comprised 64% (n = 69), eastern migrants 17% (n = 18), and resident 19% (n = 20) of the elk-years. Two males (1 eastern, 1 western migrant) made movements suggesting dispersal, but they were harvested prior to the opportunity of returning to the winter range, and so could have migrated or dispersed. Thus, we omitted these males when we analyzed migratory status. Two males switched migratory status: 1 male switched from being resident to being a western migrant, and the second male switched each of 3 years; it was a western migrant in year 1, resident in year 2, and eastern migrant in year 3.

Male elk antler size

We recorded 96 antler measurements from 72 elk captures in January, 18 collared elk and 3 uncollared elk harvested by hunters in September and October, and 3 additional elk that died between October and February in 2018–2020. We obtained antler measurements for 65 radio-collared individuals with known ages; 40 individuals were measured once and 25 measured twice in different years resulting in 90 age-specific antler measurements.

Antler size increased with age as did the number of antler points (Table 2). Less than 16% of 2–3-year-old males, 64% of 4-year-old males, and >83% of ≥5-year-old males were legal for harvest under the 6-point APR (Table 2). Using measurements from all known-aged individuals (n = 90), including captured and harvested males

(Figure 2), the top model describing antler size included a non-linear (quadratic) effect of age with a random effect for individual (BIC weight = 0.83; Table 3). In the second antler size sub-model when migratory status was known (n = 86), adding year and tactic to the best approximating model of antler size based on age (quadratic relationship), resulted in 2 models with similar weight: quadratic age plus year (Table 3; BIC weight = 0.50) and quadratic age relationship (Table 3; BIC weight = 0.49). Moreover, effects of year were statistically weak. Antler size was greatest in 2019 ($\beta year_{2019} = 38.26 \pm 30.72$ [SE]) followed by 2020 ($\beta year_{2020} = 24.55 \pm 32.10$) and 2018 ($\beta year_{2018} = 23.79 \pm 29.76$), but all years overlapped in antler size. The strength of the age effect on antler size was similar when we included the year effect into the model (age only model: $\beta_0 = 58.65 \pm 17.22$, $\beta_{age} = 64.58 \pm 9.82$, $P = 0.001$; $\beta_{age}{}^2 = -3.87 \pm 1.33$, $P = 0.008$; age and year effect model: $\beta_{age} = 79.14 \pm 17.88$, $P < 0.001$; $\beta_{age}{}^2 = -5.05 \pm 2.47$, $P = 0.044$). This confirms stability of the estimated effects of age regardless of inclusion of year. Because confidence limits of beta coefficients of year effects overlapped zero and the effects of age were robust among models, we used the quadratic age model without year or migrant class effects to predict antler sizes in the survival model. The predictive model structure, using unstandardized coefficients was:

$$\text{Antler size (inches)} = 58.65 + (64.5 \times \text{age}) - (3.87 \times \text{age}^2)$$

In the final reduced sub-model where GPS locations were available in the growing season preceding antler measurements, only 22 individuals were used to evaluate effects of summer forage biomass while accounting for age-specific differences on antler size (Table 3). The reduction in sample size arose because only collared animals that were harvested had such GPS data. The model with the quadratic effect of age alone had similar weight (BIC weight = 0.51) to the model with forage biomass (BIC weight = 0.39). Males that were exposed to higher summer forage biomass (hence lower forage quality) had smaller antlers ($\beta_{forage} = -12.19 \pm 8.06$, $P = 0.147$). Although the confidence limits of coefficients for age and forage overlapped zero because of the reduced sample of antler measurements (n = 22 vs. n = 90), the unstandardized beta coefficients for the quadratic effect of age were close to those in the age-only model reported above ($\beta_{age} = 52.83 \pm 71.33$, $P = 0.468$; $\beta_{age}{}^2 = -1.96 \pm 8.03$, $P = 0.810$).

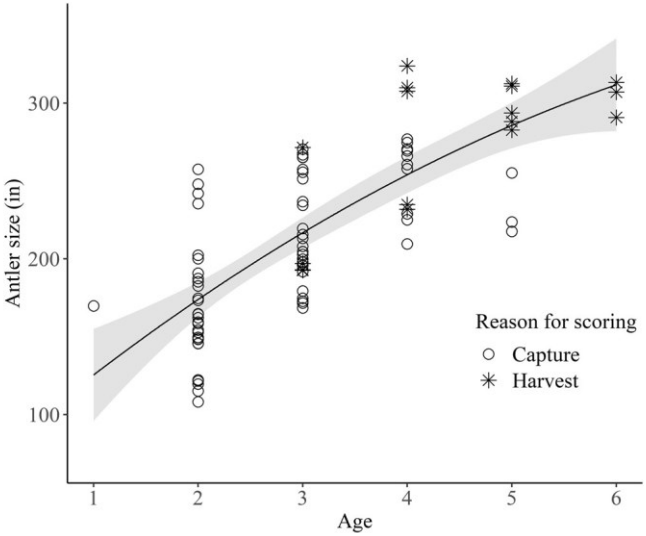

FIGURE 2 Antler size as a function of male elk age in the Ya Ha Tinda population in and adjacent to Banff

National Park, Alberta, Canada, 2017–2020. Antler size was measured using guidelines for the Safari Club International gross antler score for elk in inches (in). We measured antler size of live males during January captures (n = 90) and after harvest. There were no elk >6 years old.

TABLE 3 Model selection for models predicting male elk antler size index (Safari Club International gross score) for subsets of elk based on known elk age, migratory tactic, and summer forage. We present number of parameters (K), log likelihood (LL), Bayesian Information Criterion (BIC), and BIC weight (BICWt) for models using data from the

Ya Ha Tinda elk population in and adjacent to Banff National Park, Alberta, Canada, 2018–2020. Age class (2, 3, ≥4 yr), age (yr), migratory tactic (resident, eastern migrant, western migrant), year (2018–2020), and summer forage biomass were factors. All models included a random effect for individual elk.

Model variables	K	BIC	BICWt	LL
Age effects only (n = 90)				
Age + age^2	5	884.90	0.83	−431.20
Age	5	888.13	0.17	−435.06
Age class	8	894.85	0.01	−429.42
Age, year, tactic (n = 86)				
Age + age^2 + year	7	861.43	0.50	−415.12
Age + age^2	4	861.44	0.49	−421.81
Age + age^2 + tactic	7	873.83	0.00	−421.32
Age + age^2 + tactic + year	10	874.43	0.00	−414.94
Age, forage biomass (n = 22)				
Age + age^2	4	237.51	0.51	−112.48
Age + age^2 + forage	5	238.04	0.39	−111.18
Age + age^2 + forage + forage^2	6	240.70	0.10	−110.94

Adult male survival

We used 105 male elk-years of age-specific survival data from 70 unique individuals with classified migratory tactics. All male elk harvested by licensed or First Nations hunters occurred between 1 September and 30 November. The annual (1 Jun–31 May) Kaplan-Meier survival rate (S) for residents (S = 0.85, 95% CI = 0.60–0.95) was 0.41 higher than for eastern migrants (S = 0.44, 95% CI = 0.182–0.680) and 0.18 higher than for western migrants (S = 0.66, 95% CI = 0.54–0.77; $\chi_2^2 = 4.2$, P = 0.10). Annual survival rates differed by age class ($\chi_2^2 = 10.1$, P = 0.006; Figure 3) with 2–3-year-old males having the highest survival (S = 0.86, 95% CI = 0.69–0.94), compared to 4-year-old males (S = 0.72, 95% CI = 0.55–0.83), and ≥5 year old males (S = 0.42, 95% CI = 0.24–0.58).

The top Cox proportional hazards model describing hunting season mortality (1 September–31 November) included the effect of predicted antler size and distance to road (Table 4). Males with predicted antler size in the top quartile (>1 SD of antler scores) had a hazard ratio (HR) 2.98 times (SE = 0.76) that of the average male elk (Table 5). In unstandardized terms, for every 2.5-cm (i.e., SCI inch scale) increase in antler size, the expected mortality hazard increased by 2.5% (HR = 1.03, SE = 0.006; Figure 4). Moreover, for every kilometer that a male was located farther from a road, the expected mortality hazard decreased by 20% (HR = 0.80, SE = 0.009; Figure 5). For comparison, we also present the hazard model set with age class instead of antler size and the top-model included age class and distance to road (Tables 4 and 5). Males in the ≥5-year-old age class had an expected hazard 10.4 times (HR = 10.44, SE = 6.32) that of the 2–3-year-old age class (the reference age class; Table 5).

We recorded 36 uncensored mortalities of 75 radio-collared male elk over the 105 elk-years. Most harvest was concentrated on the Ya Ha Tinda winter range in WMU 418 where 27 males were harvested (Figure 1). In comparison, the harvested number of males in other WMUs were 1 male in 314, 318, and

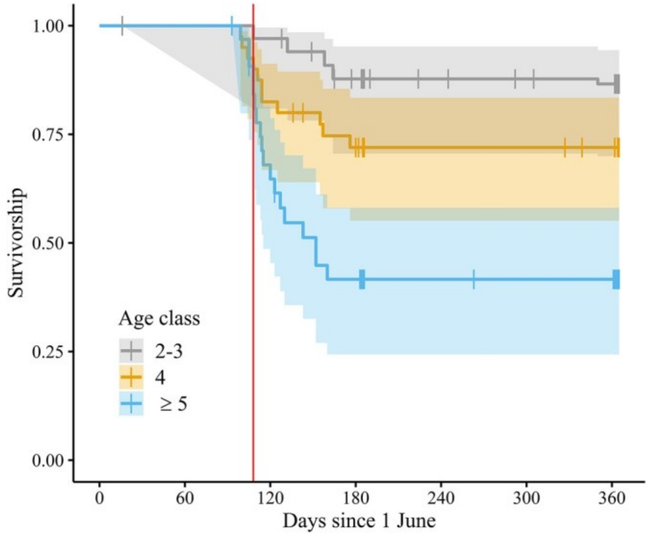

FIGURE 3 Annual (1 Jun–31 May) Kaplan-Meier survivorship curves for 3 age classes (2–3, 4, and ≥5 yr) in the Ya Ha Tinda population in Alberta, Canada, 2018–2020. Rifle hunting season begins on 17 September (denoted by the red vertical line) and archery season begins on 25 August.

TABLE 4 Model selection results for the effects of antler size versus age on survival of male elk from Cox proportional hazards models of survival in the Ya Ha Tinda elk population in and adjacent to Banff National Park, Alberta, Canada, during the hunting season (1 Sep–30 Nov) in 2018–2020. We tested effects of antler size (standardized, predicted Safari Club International score [PScore]), elk age class (2–3, 4, ≥5 yr), standardized distance to road (km; dist road), antler point restriction (APR; 6-point vs. 3-point) of each elk location, and migratory tactic (resident, eastern migrant, western migrant). We predicted PScore from an age + tactic antler size model. We present number of parameters (K), log likelihood (LL), Bayesian Information Criterion (BIC), and BIC weight (BICWt). All models included a random effect for individual.

Model names	K	BIC	BICWt	LL
Survival – antler size PScore + dist road	3	268.83	0.984	−121.47
PScore + dist road + APR	4	277.25	0.015	−121.36
PScore × APR	4	282.42	0.001	−123.95

PScore + APR	3	283.23	0.001	−128.67
PScore + tactic	5	298.67	0.000	−127.75
Survival – age class				
Age class + dist road	4	292.221	0.985	−128.715
Age class + dist road + APR	5	300.804	0.013	−128.658
Age class + APR	4	305.625	0.001	−135.417
Age class × APR	6	313.531	0.000	−130.673
Age class + APR	6	325.896	0.000	−136.856

TABLE 5 Beta coefficients and hazard ratios (HR) of the top Cox proportional hazards models of effects of antler size versus age on male elk mortality in the Ya Ha Tinda population (n = 105 elk years, 33 mortalities) in and adjacent to Banff National Park, Alberta, Canada, 2018–2020. Because antler size and age were strongly correlated, we compared contrasting models of the effects of antler size versus age class, along with distance to road, on survival. Covariates were 3 categories of age, 4-year (age 4) and ≥5 year (age ≥5) age classes (1–3-yr-old age class was the baseline hazard reference category), distance to road (dist road; m), and predicted Safari Club International Gross score of antler size (PScore). We standardized Pscore and dist road prior to analysis and report here hazard ratios in units of standardized covariates.

Variable	Beta	SE	HR[a]	SE(HR)	P
Mortality PScore	1.092	0.255	2.979	0.760	<0.001
Dist road	−2.286	1.114	0.102	0.114	<0.001
Mortality					
Age 4	1.219	0.613	3.385	2.075	0.047
Age ≥5	2.345	0.606	10.437	6.325	<0.001
Dist road	−2.346	1.085	0.096	0.104	0.031

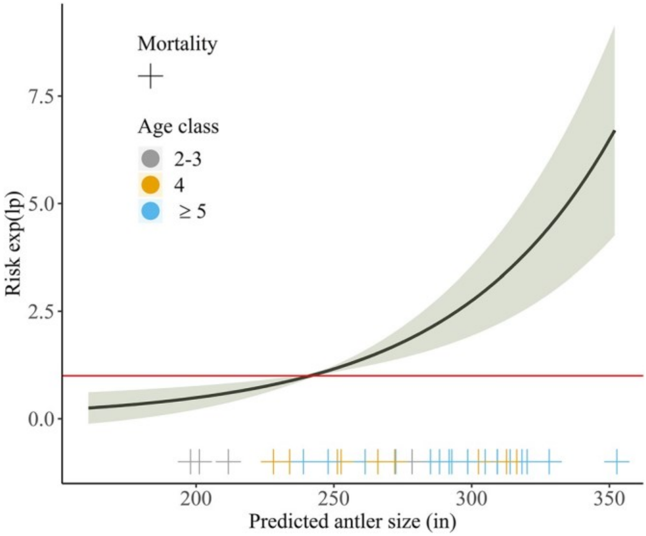

FIGURE 4 Relative risk of harvest expressed as the hazard ratio (exp(lp), lp = linear predictor from the top model) and 95% confidence interval (gray shading) for harvested male elk (by all harvest types) as a function of predicted antler size (Safari Club International [SCI] gross score in inches [in]) during the hunting season (1 Sep–30 Nov) in the Ya Ha Tinda population in Alberta, Canada, 2018–2020. Note antler size (SCI score) was predicted for male elk in subsequent biological years following capture using a generalized linear mixed effect model of the relationship between age and antler size. The ages and antler score of harvested males (n = 35) are represented by crosses with colors for each age class (2–3, 4, and ≥5 yr) and the horizontal red line represents a hazard ratio of 1, above which risk of harvest increased.

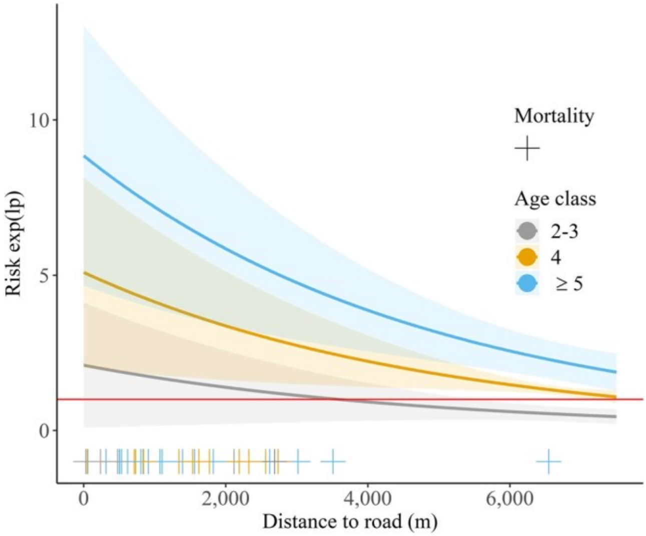

FIGURE 5 Relative risk of harvest expressed as the hazard ratio (exp(lp), lp = linear predictor from the top model) and 95% confidence interval (shading) for the average predicted antler size (Safari Club International [SCI] gross score) of harvested male elk (by all harvest types) in each age class (2–3 years old, 206.69 inches; 4 years old, 257.92 inches; and ≥5 years old, 289.91 inches) over the range of distances from roads during the hunting season (1 Sep–30 Nov) in the Ya Ha Tinda herd Alberta, Canada, 2018–2020.

412, and 2 males in WMU 316 and 417. Most mortalities were caused by humans (20 recreational harvest, 11 First Nations harvest, 2 wounding losses [1 associated with recreational and 1 associated with First Nations harvest]), with only 1 mortality from starvation, and only 2 killed by wolves. There were no male elk killed by grizzly bears. We compared traits of elk harvested by the 2 main sources, First Nations and licensed harvest within WMU 418 where most of the harvest occurred and with the 6-point APR. There were no differences ($t_{22.94} = 1.22$, $P = 0.236$) in the distances from roads of elk harvested by First Nations (n = 9 with known spatial locations; 1,422 m, SD = 942.6) or licensed hunters (n = 17; 2,002 m, SD = 1,477.5). Predicted antler size of elk harvested by First Nations (SCI score = 299, SD = 24.4) and licensed hunters (SCI score = 277, SD = 37.9) were not different ($t_{8.12} = 1.41$, $P = 0.195$), nor were there differences ($t_{10.809} = 1.89$, $P = 0.086$) in age of elk (First Nations ages = 4.6, SD = 0.74; licensed hunter ages = 4.8, SD = 0.75), or timing of harvest (First Nations ordinal date = 272, SD = 22; licensed hunter ordinal date = 275, SD = 22; $t_{15.96} = 0.34$, $P = 0.734$). Because of the lack of differences, we did not formally test for differences in survival models.

Overall, the annual mortality due to recreational harvest was the leading cause of death (CIF = 0.203, 95% CI = 0.129–0.303), followed by First Nations harvest (CIF = 0.101, 95% CI = 0.053–0.173), wolf-caused mortality (CIF = 0.015, 95% CI = 0.002–0.051), and malnutrition (CIF = 0.005, 95% CI = 0–0.030). Cause-specific mortality did not differ between migratory tactics, rejecting the prediction that western migrant elk summering in the protected national park would experience lower hunter mortality (harvest Gray's test $Q_{gray} = 2.039$, $P = 0.361$, First Nations $Q_{gray} = 2.501$, $P = 0.285$, wolf $Q_{gray} = 1.720$, $P = 0.423$; Table 6). First Nations harvest was the only CIF different between years (wolf $Q_{gray} = 2.50$, $P = 0.286$; harvest $Q_{gray} = 0.92$, $P = 0.630$, First Nations $Q_{gray} = 20.00$, $P < 0.001$; Table 6) with it being higher in 2020 (CIF = 0.232, 95% CI = 0.111–0.414) compared to 2019 (CIF = 0.029, 95% CI = 0.004–0.095) and 2018 (CIF = 0).

TABLE6 Annual(1Jun – May)cumulativeincidencefunctions(CIF)ofcause -specificmortalityrates(i.e.,probability)formigratorytacticsandbyyearofmortalityof maleelkintheYaHaTindapopulation,inandadjacenttoBanffNationalPark,Alberta,Canada,2018 – 2020.Theloweranduper95%log -logconfidenceintervals(LCI −UCI) arereported.Gray'stestfordifferencesbetweenmortalitysourcesbymigrationtacticoryearrevealedthatonlyFirstNations(FN)harvestdiffer edbetweenyears.

	Fate											
	MalnutritionWolfHarvestFNharvest											
	n	CIFLCI	−UCI	n	CIFLCI	−UCI 2020	n	CIFLCI	−UCI	n	CIFLCI	−UCI
Migrationtactic												
31 Residents000030.1350.03									−0.36500			
Eastern0010.0780.003						−0.43860.3170.118			−0.66220.0910.014			−0.327
Western0010.0110						−0.058130.1940.105			−0.32180.1170.053			−0.220
Year												
201810.0130.001			−0.0700080.1390.061						−0.26600			
20190020.0310.004						−0.010100.1630.082			−0.29220.0290.004			−0.095
2020000040.1150.040									−0.24890.2320.110			−0.414

DISCUSSION

Our study contributes to our understanding of the key relationship between age and antler size of free ranging North American elk (Wolfe 1982) and showed that antler size is primarily driven by male elk age. While choice of migratory tactic itself did not lead to enhanced survival or antler size, we found evidence that higher forage quality experienced by migrants enhanced antler size consistent with the forage maturation hypothesis (Fryxell 1991). Western migrants with greater access to higher forage quality had predicted antler sizes that were 57 cm and 33 cm greater compared to eastern and resident males, respectively. This difference is equivalent to a > 1-year growth difference between 5- and 6-year-old males, which is biologically significant because the strongly size-selective harvest in our population limits the number of 6-year-old males. Moreover, more males (64%) than females (10%) chose high-quality, western summer ranges (Martin 2021), also lending support to the benefits of migration for males. Because choice of western migratory tactic enhanced body condition, pregnancy, and 6-month-old calf weights (Hebblewhite et al. 2008), the nutritional advantage for male elk to migrate west is consistent with maximizing antler growth. Indeed, antler size is often correlated to reproductive success in cervids (Clutton-Brock et al. 1980, 1982; Bartoš and Bahbouh 2006; Morina et al. 2018; Markussen et al. 2019). While speculative, our work is consistent with the predictions of the forage maturation hypothesis that western migrant males may also have higher reproductive success resulting from larger antler size. Yet given the high harvest we report, such bottom-up differences in reproductive success may be limited, and breeding may be by younger males (Noyes et al. 1996). Few studies have addressed these questions in wild free-ranging elk, however, though we are currently developing a wild pedigree based on these radio-collared males to test these questions (Pemberton 2008).

We found that human harvest by recreational and First Nations hunters was the major source of mortality on male elk. We expected wolf predation would be a primary cause of mortality in males because wolves are the leading cause of mortality for female elk in our system (Hebblewhite and Merrill 2011, Hebblewhite et al. 2018), but wolves only killed 2 males in our study. While grizzly bears were the second leading cause of non-human predation on adult female elk in our study, they killed no male elk. The low wolf predation we observed is in contrast to male elk in Yellowstone National Park where males were strongly selected by wolves and comprised up to 40% of wolf kills in the winter (Metz et al. 2012). Metz et al. (2012) reported that male elk killed by wolves in winter in Yellowstone, where hunting is prohibited, were often older (up to 12 years of age) and more likely to have fat-depleted bone marrow (<70% bone marrow fat) than females killed by wolves, or male elk killed by wolves in Paradise Valley, Montana, USA, where they are hunted (Wright et al. 2006). This suggests that wolves often kill older vulnerable males following the rut when they are nutritionally stressed. Yet in our study, few males survived to such older ages because of harvest. Thus, hunting likely reduces the availability of vulnerable male elk for wolf predation post-rut because survival is low past 6 years of age (Metz et al. 2012, 2020). Alternatively, lower wolf predation on male elk in our study may occur because wolves face much higher harvest pressure from hunting and trapping outside Banff National Park (Smith et al. 2016, Hebblewhite and Whittington 2020). But if wolf harvest reduced wolf predation, we would have expected wolf predation also be low on female elk, yet wolf predation remained the leading cause of female mortality during this study (i.e., Hebblewhite et al. 2018). Collectively, this suggests wolf predation on male elk may be important only in protected areas where there are more abundant older male elk that are more vulnerable to wolves. Despite our high-predation study area, wolves were not competing with human hunters for male elk harvest, though high predation by grizzly bears especially on neonatal elk may also limit male elk for harvest (Berg et al. 2023).

Migration itself did not affect male survival, despite 64% of males using western summer ranges in Banff National Park with no hunting. We think this is because of the timing of migration relative to rut and hunting. The rifle hunting season typically occurs between 17 September and 31 November, whereas most (>50%) male elk using summer ranges in Banff National Park have migrated by 15 September (Martin 2021) following the early female migration during rut, and thus becoming exposed to harvest. Bighorn sheep show similar timing of migration outside parks in Alberta, such that these protected areas do not provide a refuge from harvest (Pelletier et al. 2014, Poisson et al. 2020). In contrast, 90% of eastern migrants returned to Ya HaTinda before the 3-point hunting season opened (1 Nov); therefore, we did not see higher harvest rates of eastern migrants compared to other migratory strategies. Most eastern migrant elk were harvested after migration in the mountain WMUs with 6-point APRs (Figure 1). Thus, while others reported differences in harvest between migratory tactics, for example, red deer (Cervus elaphus) in Norway (Rivrud et al. 2015, Loe et al. 2016), and elk in the Greater Yellowstone Ecosystem (Smith 2007), it often is the timing of harvest that influences differential harvest effects on migratory tactics.

Our study indicates how APRs influence age-specific survival rates of male Rocky Mountain elk (C. c. nelsoni). Survival rates we observed for 2–3-year-old males (S = 0.86, 95% CI = 0.69–0.94) are consistent with unharvested populations of subadult (1–2 yr) males in eastern North America (S = 0.85; Keller et al. 2015). In contrast, the survival rates of 4-year-old males (S = 0.72, 95% CI = 0.55–0.83) were higher than adult males in populations harvested under unrestricted hunting (i.e., no APR) in north central Idaho, USA (S = 0.60; Unsworth et al. 1993). Our survival analysis revealed low survival of ≥5-year-old males (S = 0.42, 95% CI = 0.24–0.58). These low survival rates are more similar to the survival of yearlings in areas with spike-only harvest (e.g., in Washington, USA, S = 0.41; McCorquodale et al. 2011). Survival of male elk in harvested populations without APR-type regulations ranges from 0.23 (Smith et al. 1994) to 0.63 (McCorquodale et al. 2003) with the average survival rate of adult males across studies being 0.51 (Unsworth et al. 1993, Smith et al. 1994, Biederbeck et al. 2001, McCorquodale et al. 2003, Hegel et al. 2014).

The 6-point APR enhances survival of young elk in our study area but strongly limits survival of males above this size threshold (Figure 2). Antler restrictions are often thought of as a tool to maximize quality and quantity of large males by limiting harvest. In our system, long-term success of this limited-quota harvest was close to 100% of licensed recreational hunters (R. Corrigan, Alberta Environment and Parks, unpublished data). Most 6-point males appear to be harvested each year in our population. The 6-point APR in our study did not allow males to survive to 7–10 years when they would reach maximum antler size and potentially be classed as a trophy animal by record-book criteria (Wolfe 1982, Strickland et al. 2001, Bender et al. 2003). We recorded only a handful of males with SCI gross scores >350 inches, one metric of trophy status (Figure 2). Effectiveness of APRs in achieving trophy-sized males may be more difficult for elk compared with other ungulates. For example, APRs for white-tailed deer and mule deer limit harvest on 2–3-year-old males but put more harvest pressure on 4–5-year-old males (Wolfe 1982, Bender and Miller 1999, Strickland et al. 2001, Zornes et al. 2018). The 20% annual harvest rate of males in our study would produce large-antlered white-tailed deer because their antler size increases to 5 years of age (Strickland et al. 2001) but not large-antlered elk because elk antler growth increases until age 10 (Bender et al. 2003, Hewitt et al. 2014). Thus, the probability that a male elk will reach their maximum asymptotic antler growth potential at 10 years old is even more sensitive to harvest rates than for deer. Regardless of APRs, hunters often are selective for larger antlered and heavier males (Martınez et al. 2005, Mysterud et al. 2006). These examples illustrate the challenges of using APRs to maximize trophy production for elk.

As an alternative to simply reducing quotas or licenses, management strategies that limit the success of hunters may provide a better approach to allow males to escape into older, large-antlered age classes (Wolfe 1985). Adjusting the timing of the start of the rifle season later could make males harder to harvest later in rut, as would limiting road access to reduce success. The reduced risk of males being harvested farther from roads in our study corroborates results across North America (Unsworth et al. 1993, Cooper et al. 2002, McCorquodale et al. 2003). Still, where access is easy, as is in our study area, the mean distance male elk were harvested from secondary (unpaved) roads was about 1.5 km (range = 29–6,545 m), indicating hunters are potentially willing and able to travel farther from secondary roads to hunt. Road sanctuaries can be even more effective. For example, the road sanctuary along the main access road in WMU 418 (Figure 1) was 100% successful in preventing any radio-collared males from being harvested within 365 m of the road. Increasing the road sanctuary width may increase survival of males to older age classes, and thus larger antler sizes. But changes to timing of harvest and increasing road buffers would likely come at the cost of limiting harvest rates, and potentially hunter satisfaction. Alberta hunters currently must apply for an average of >10 years for the opportunity to hunt in WMU 418. High harvest success may be important to maintain hunter satisfaction, given the high demand, highlighting the challenge of trophy management for elk.

A novel contribution our study was understanding the harvest of elk by treaty First Nations, an area of growing importance for wildlife management in North America (Stricker et al. 2020). Indigenous harvest rights year-round and on both sexes are guaranteed in our study area to recognized First Nations, although not in road sanctuaries or Banff National Park. First Nations harvest rates of adult females have been a consistent but modest source of mortality in our study since 2001 (19% of all mortality; CIF = 0.0163, 95% CI = 0.008–0.03; Hebblewhite et al. 2018). First Nations harvest of female's peaks in December but also increased during the 3 years of our male elk study. Harvest of male elk by First Nations was second to licensed harvest but was higher in 2020, which may have been a result of concerns over food security during the Covid-19 pandemic (Deaton and Deaton 2020). Our data revealed no differences in elk age, antler size, spatial location (e.g., distance from road), or timing of harvest between First Nations and licensed recreational hunters. This suggests similar selection for male elk by First Nations and licensed recreational hunters in this population. Indigenous harvest rights are at a transitional stage throughout North America, where they have been historically overlooked and not explicitly integrated into the North American model of wildlife management (Hessami et al. 2021). First Nations are asserting their treaty rights for all wildlife in Canada (Mulrennan and Scott 2005), and increasing harvests on many species. Yet for other species, such as endangered woodland caribou (Rangifer tarandus caribou), they are voluntarily limiting harvest and leading caribou recovery (Lamb et al. 2022). This is a pivotal time in wildlife management where First Nations rights are being legally acknowledged and being integrated into provincial wildlife management to uphold the Canadian constitutional requirement for First Nations consultation under section 25 of the Canadian Charter of Rights and Freedoms. Cause-specific mortality data on elk from our study could help with quantitative estimates of First Nations harvest and encourage consideration of innovative harvest regulations (e.g., road sanctuaries, enhanced First Nations governance of harvest) to ensure sustainable harvests across hunters of all backgrounds.

MANAGEMENT IMPLICATIONS

The first management implication from our study is that male elk survival was not strongly influenced by large carnivore predation. This was surprising given that this elk population was limited by high wolf and grizzly bear predation rates on adult females and calves, respectively (Hebblewhite et al. 2018, Berg et al. 2023). Predation by wolves and grizzly bears may not necessarily compete with hunter opportunity for trophy-size male elk even in rich multi-carnivore systems. Second, hunting seasons that coincide with the rut limited differential harvest rates of male elk in different migratory tactics and reduced survival to older age classes, even when summer ranges were in protected areas. Third, APRs can be successful in protecting young age classes of male elk. But the increased harvest pressure on older age classes prevented males from growing old enough to maximize antler size if trophy quality is a goal of management. Fourth, the increased mortality risk closer to roads supports efforts to enhance road closures as a successful management strategy to provide security cover for hunted elk populations. Finally, our study highlights that integrating First Nations harvest into management of male elk harvest where treaty rights exist will be important to ensure sustainable management of male elk harvest in the future.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animal handling was approved through University of Montana Institutional Animal Care and Use Committee (protocol: 059-08MHECS-120908), University of Alberta Animal Care and Use Committee (Animal Use Protocol AUP 00000624), a Parks Canada Research Permit (YHTR-2017-26977), and Alberta Environment and Parks Research and Collection permits (20-004 and #20-00).

DATA AVAILABILITY STATEMENT

The male elk survival and antler size data sets are available on our Long Term Research in Environmental Biology Ya Ha Tinda elk project data archive website on Dryad at https://doi.org/10.5061/dryad.6wwpzgmw7. The R code for the male elk survival model(s) is available on Zenodo at https://zenodo.org/record/7135259.

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