BioOne COMPLETE

Survival and Recovery Estimates of Male Elk in a Harvested Inter-Jurisdictional Population

Authors: Hegel, Troy M., Gates, C. Cormack, and Eslinger, Dale

Source: Wildlife Biology, 20(1) : 57-63

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.13010

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Communications

Wildlife Biology 20: 57–63, 2014
doi: 10.2981/wlb.13010
© 2014 The Authors. This is an Open Access article
Subject Editor: Erlend B. Nilsen. Accepted 20 August 2013

Survival and recovery estimates of male elk in a harvested inter-jurisdictional population

Troy M. Hegel, C. Cormack Gates and Dale Eslinger

T. M. Hegel (troy.hegel@gov.yk.ca) and C. C. Gates, Faculty of Environmental Design, Univ. of Calgary, PO Box 2500, University Drive N.W., Calgary, AB, T2N 1N4, Canada (TMH, CCG), and Inst. of Arctic Biology, Univ. of Alaska Fairbanks, Fairbanks, AK, 99775, USA (TMH). Present address for TMH: Fish and Wildlife Branch, Yukon Department of Environment, PO Box 2703, Whitehorse, YT, Y1A 2C6, Canada. – D. Eslinger, Fish and Wildlife Division, Alberta Environment and Sustainable Resource Development, 346-3 Street S.E., Medicine Hat, AB, T1A 0G7, Canada

Demographic rates are critical pieces of information for understanding ungulate population dynamics and effectively managing populations. In harvested elk *Cervus elaphus canadensis* populations, human harvest is often the greatest source of adult male mortality. In the Cypress Hills of southeast Alberta and southwest Saskatchewan, Canada, hunting is a tool to mitigate conflicts between elk and agricultural producers in the area. We estimated survival (S) and animal recovery (f) rates based on individually marked male elk (n = 47) using hunter-returned ear tags from 1998–2001. Recovery rate differed between jurisdictions and was substantially lower in Saskatchewan (f = 0.16, SE = 0.05) compared to Alberta (f = 0.31, SE = 0.08). A constant survival rate (S = 0.61, SE = 0.15) was most supported. The average longevity for male elk in the Cypress Hills was 2.02 (SE = 0.51) years after surviving their first year of life. This research highlights the importance of considering regulatory regimes and requirements when investigating and interpreting demographic and population dynamics of populations managed across jurisdictions.

Demographic parameters are critical information for effective wildlife management (Caughley 1977, Williams et al. 2001). They can be used as components in population models (Buckland et al. 1996, Langvatn and Loison 1999), to assess population responses to management actions (Biederbeck et al. 2001, Murrow et al. 2009), and to gain insight into causal mechanisms surrounding population change (Kimball and Wolfe 1974, Coulson et al. 2005). Variability in demographic parameters can occur due to environmental stochasticity (Garrott et al. 2003), age (Jorgenson et al. 1997) and sex structure effects (Toïgo and Gaillard 2003), spatial variability (Pettorelli et al. 2002, Grøtan et al. 2009), and management actions (Bender and Miller 1999). Understanding the source of variation can be useful for management decision-making.

Adult female survival is typically the most influential parameter determining future population growth rate; whereas juvenile survival often explains the most variation in observed population growth rates (Gaillard et al. 1998, 2000). However, male demography can also influence ungulate population dynamics (Mysterud et al. 2002, Rankin and Kokko 2007) through male contributions to population density (i.e. influencing density-dependent processes), and the effect of adult sex ratio and male age structure on female breeding success and/or timing of parturition (Mysterud et al. 2002). Hunting is often the greatest source of male mortality in harvested ungulate populations (Raedeke et al. 2002), and thus mortality rates should be monitored to ensure harvest is sustainable (Gordon et al. 2004).

The Cypress Hills elk *Cervus elaphus canadensis* population in southeast Alberta and southwest Saskatchewan, Canada (Fig. 1), is harvested to mitigate elk damage to agricultural resources (Hegel et al. 2009). Elk were native to the Cypress Hills, however by the early 1900s hunting pressure had extirpated them from the area (Soper 1946). In the 1930s approximately 25 elk were reintroduced to the Cypress Hills in Saskatchewan (Keith 1977). Subsequently, by 2000 the elk population increased in size to approximately 1100 (Alberta Fish and Wildlife Division, unpubl.), and expanded its range westward throughout the Cypress Hills (Hegel et al. 2009). During aerial surveys (1998–2001) the proportion of the population observed in Alberta ranged from 0.30 to 0.50 (Alberta Fish and Wildlife Division, unpubl.). The population was non-migratory and occurred year-round in the Cypress Hills. The female portion of the population was spatially structured into six subpopulations (Hegel et al. 2009). There is no information available regarding male spatial structuring.

This increase in size and distribution resulted in conflicts (Redpath et al. 2013) between the Cypress Hills agricultural community and the elk population foraging on valuable

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

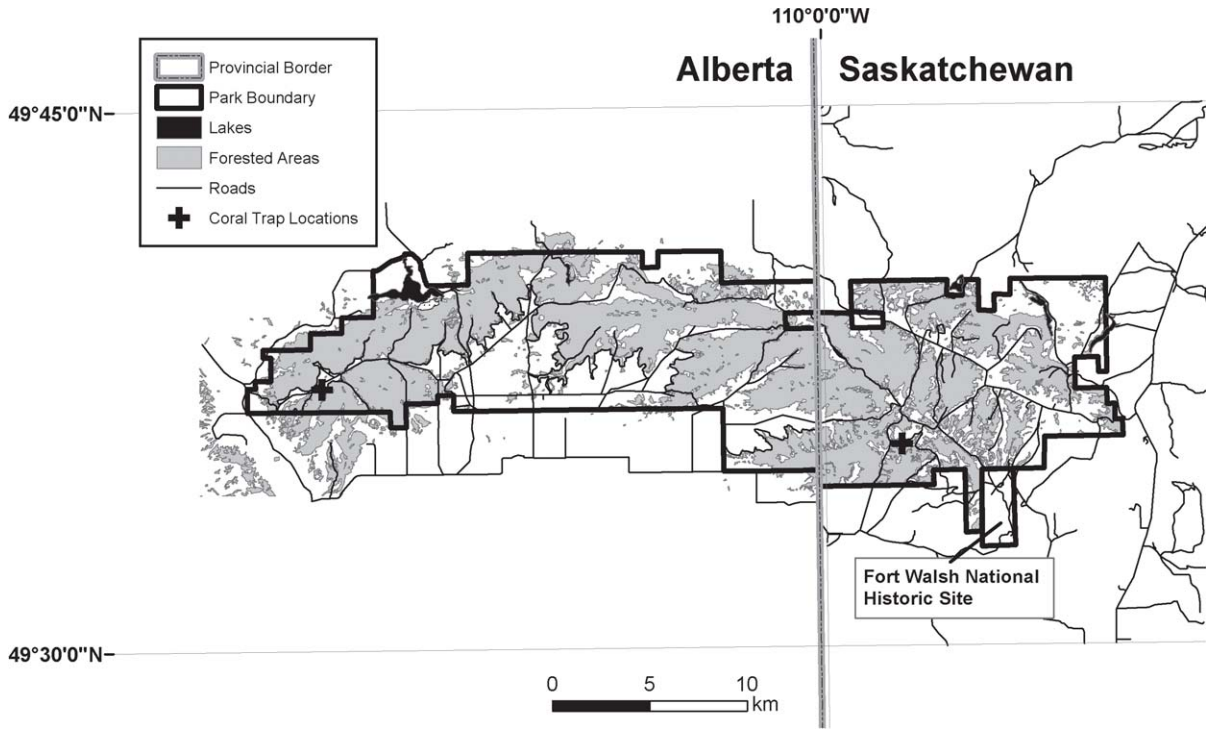


Figure 1. Location of Cypress Hills Interprovincial Park in Alberta and Saskatchewan, Canada. The Alberta portion of the Park is called the Elkwater Block and the Saskatchewan portion is called the West Block.

agricultural resources, damaging fences, competing with livestock for range, and feeding on stacked hay. Consequently, annual management hunts (i.e. a harvest implemented to achieve a specific management objective; Connelly et al. 2012) were initiated in both Alberta and Saskatchewan to mitigate agricultural conflicts and reduce the elk population to a management target (Chee and Wintle 2010) of 700 individuals. Harvest management of the Cypress Hills elk population is complicated by its relatively unique geography in that it ranges in three jurisdictions with a mosaic of public and private lands.

Management hunts were administered separately in Alberta and Saskatchewan. From 1998–2001, Saskatchewan annually issued 200 elk permits, allowing hunters to take an animal of either sex, including calves, from October–December. Aboriginal harvest (i.e. constitutionally protected subsistence hunting by Canada's aboriginal peoples) also occurred year-round in the area with no provincially issued hunting license required. From 1998–2001, Alberta issued between 201 and 305 either-sex (calves included) permits, in addition to a number of antlerless-only (cows and calves) permits, for the hunt occurring from October–January. In both jurisdictions hunting was allowed inside CHIP, but hunting was prohibited within Fort Walsh National Historic Site. Aboriginal harvest also occurred in Alberta, with all hunters (aboriginal and non-aboriginal) required to obtain a firearm discharge permit if hunting in the Elkwater Block (Fig. 1). In Alberta, hunters were required to register their kill with Parks staff, and from 34 to 58 bulls were harvested annually from 1998–2001. In these years, bulls represented 48% to 59% of the total harvest by hunters with either-sex permits (Alberta Fish and Wildlife Division, unpubl.). Harvest reporting was voluntary in Saskatchewan.

Information regarding survival rates in this population is lacking but may be valuable for assessing the success of the management hunt and ensuring long-term conservation of the population (Bunnefeld et al. 2011). The objective of this research was to assess the influence of age class, annual variability, and spatial distribution on male survival in the Cypress Hills.

Methods

Study area

The Cypress Hills are located along the border of southern Alberta and Saskatchewan, Canada (Fig. 1). The area consists of Cypress Hills Interprovincial Park (CHIP; ~ 350 km^2) and adjacent private and public lands. The Alberta and Saskatchewan portions of CHIP are termed the Elkwater and West Blocks, respectively. Adjacent to the West Block is Fort Walsh National Historic Site (~ 6.5 km^2) managed by the federal Parks Canada Agency. Domestic cattle graze in CHIP from June to October, while private lands surrounding CHIP support year-round livestock grazing as well as forage and cereal crop production, and native rangelands.

The Cypress Hills form an outlying upland of a partially unglaciated high plateau that is deeply dissected by narrow coulees and valleys. The area rises sharply to 600 m above the surrounding prairies. Elevation of the plateau declines gradually from a western summit of 1465 m to 1310 m in the east. The high elevation of the Cypress Hills results in a cooler and moister climate than the surrounding plains, effectively forming a partially forested island surrounded by grassland prairie and cultivated agricultural crops (e.g. alfalfa). Mean

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

annual precipitation during 1981–2000 was 607.0 mm, with mean July and January temperatures of 15.4°C and –9.5°C, respectively (Environment Canada 2000). Breitung (1954), Newsome and Dix (1968), and Widenmaier and Strong (2010) provide detailed descriptions of the vegetation in the area.

Animal capture

During the winters (January/February) of 1998 and 1999, a portable corral trap was erected in the West (Saskatchewan) and Elkwater (Alberta) Blocks, respectively. The 1998 and 1999 trap locations were located approximately 30 km apart (Fig. 1). Animals were lured into the corral with salt and alfalfa hay. Once a group of animals was in the corral, a technician closed the entrance gate via remote control. Males born the preceding spring (i.e. short-yearlings) were handled in a sorting tub and fitted with uniquely numbered ear tags to identify animals. Tags were placed in both ears to minimize tag loss which can negatively bias survival estimates (Nelson et al. 1980). Animals were handled in accordance with approvals obtained from the Univ. of Calgary Animal Care Committee (Protocol BI2001-065) and an Alberta Sustainable Resource Development Wildlife Research Permit and Collection License.

Survival analysis

We adopted a capture–mark–recapture framework (Lebreton et al. 1992) using band-recovery models (Brownie et al. 1985) of hunter returned ear tags from 1998–2001 to estimate survival (S) and recovery (f) rates for male elk. Recovery represents the probability that a tagged animal was killed (K), retrieved by a hunter (c), and reported (λ), such that $f = K c \lambda$. Natural (i.e. non-harvest) mortality plus unreported harvest mortality is thus $m = 1 - S - f$.

Candidate models were specified to reflect a variety of factors potentially influencing both S and f. Annual variability (t) was included, as both survival and harvest rates could be influenced by variation in, for example, annual climatic conditions affecting natural mortality or environmental conditions during the hunting season influencing hunter success rates. We defined a year as ranging from 1 February to 31 January. As all captured animals were the same age (i.e. male calves) we could not assess age-specific survival (Anderson et al. 1985, Brownie et al. 1985). We tested whether animals differed in S and f for the year following capture ($Yr1$) relative to subsequent years. Due to differences in harvest management in Alberta and Saskatchewan, we also included a model representing group (g) differences based on an animal's capture location. This model also represents a cohort effect (Rose et al. 1998) as all individuals captured within a year were of the same age. Finally, we included models representing constant (i.e. S.) rates for S and f. Candidate models were ranked using Akaike's information criterion adjusted for small sample size (AICc), with the model having the lowest AICc value being most supported (Burnham and Anderson 2002). Goodness of fit, $\hat{c} = \chi^2$ / DF, was assessed on the most general model, where χ^2 and DF are the model's deviance and degrees of freedom, respectively. If $\hat{c} > 1$ overdispersion, or lack of fit, is occurring and model selection values (i.e. AICc) were adjusted resulting in quasi-AICc values (QAICc; Burnham and Anderson 2002).

Analysis was carried out using Program MARK, ver. 6.2 (White and Burnham 1999). A logit link function was used for all models. Variances for derived parameters such as m and mean lifespan [MLS = -1 / $\log_e(S)$; Seber 1982] were calculated using the Delta method (Bolker 2008).

Results

We captured 31 and 16 male calves in corral traps and fitted them with ear tags in 1998 (Saskatchewan) and 1999 (Alberta), respectively. Of the animals captured in 1998, five, three, two, and one were recovered from 1998 to 2001. From the animals captured in 1999, five, three, and two were recovered from 1999 to 2001. All recovered animals were harvested in the province in which they were captured.

The model most supported by the data (Appendix 1) represented constant survival and separate recovery rates in Alberta and Saskatchewan (i.e. $S. f_g$). The most general models had a $\hat{c} < 1.0$, indicating no lack of fit to the data (Lebreton et al. 1992) and thus AICc values were not adjusted. The estimated survival rate was 0.61 (SE = 0.15) and the estimated recovery rates in Alberta and Saskatchewan were 0.31 (SE = 0.08) and 0.16 (SE = 0.05), respectively. Natural mortality (and non-recovery) rates (m) were 0.08 (SE = 0.11) and 0.23 (SE = 0.16) in Alberta and Saskatchewan, respectively. The average longevity (MLS) of male elk in the Cypress Hills was 2.02 (SE = 0.51) years following capture.

Discussion

Our estimate of male elk survival in the Cypress Hills was based on animals aged one through four and was constant over time and space. Survival of male elk in our study was similar to other hunted populations across North America and substantially lower than non-hunted populations (Table 1). Due to age-specific survival rates reported in other ungulate populations (Loison et al. 1999), differing survival for the youngest age class of marked elk (i.e. $Yr1$) was tested. However, similar to other harvested elk populations (Unsworth et al. 1993, McCorquodale et al. 2003) our data did not support age-class specific survival, at least with respect to the year following capture.

The constant survival rate is also consistent with male elk and red deer *C. elaphus* survival reported elsewhere (Unsworth et al. 1993, Loison and Langvatn 1998, McCorquodale et al. 2003). This may be due to the marked animals in our study being at or approaching their peak body size (Festa-Bianchet 2012) and thus in good physical condition. Additionally, the intensive harvest of elk in the Cypress Hills may have maintained the population at sufficiently low densities such that bottom-up factors were a weak regulatory force. Forage limitation would be further reduced given the high quality agricultural resources (e.g. alfalfa, oats) used seasonally by elk in the lands surrounding CHIP (Hegel et al. 2009), which may act as a form of supplementary feeding (Smith 2001). Finally, given that harvest is the primary source of male mortality in harvested elk populations (Raedeke et al. 2002) and

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Reported annual survival rates of male elk populations across North America based on estimates from marked animals.

Survival rate (SE)	Location	Years	Hunted	Source
0.92 (0.04)	Kentucky, USA	1998–2001	no	Larkin et al. 2003
0.911 (0.021)	North Carolina, USA	2001–2006	no	Murrow et al. 2009
0.83 (95% CI: 0.76–0.88)	Washington, USA	2003–2006	yes	McCorquodale et al. 2011
0.68 (n/a)	Montana, USA	1938–1955	yes	Peek et al. 1967
0.63 (0.05)	Washington, USA	1992–1999	yes	McCorquodale et al. 2003
0.61 (0.15)	Alberta/Saskatchewan, Canada	1998–2001	yes	this study
0.600 (0.063)	Idaho, USA	1986–1991	yes	Unsworth et al. 1993
0.58 (0.02)	Utah, USA	1951–1960	yes	Kimball and Wolfe 1974
0.57 (0.10)	Oregon, USA	1994–1998	yes	Biederbeck et al. 2001
0.55 (0.10)	New Mexico, USA	1978–1981	yes	White 1985
0.5362 (0.0512)	Wyoming, USA	1958–1960	yes	Sauer and Boyce 1983
0.503 (0.003)	Wyoming, USA	1991–1994	yes	Smith and Anderson 1998
0.3776 (0.0950)	Wyoming, USA	1951–1952	yes	Sauer and Boyce 1983

that the availability of tags in both provinces was relatively static from 1998–2001, the managed hunt may also have contributed to constant survival as recovery rates did not vary annually (Appendix 1).

Mean lifespan, in this analysis, represents the average number of years a male elk would be expected to live after reaching one year of age. Projecting survival rates into the future, upon reaching one year of age male elk had a probability of 0.08 and <0.01 of surviving five and 10 years, respectively (Fig. 2). Given reduced annual survival rates of old (senescent) animals (Loison et al. 1999, Murrow et al. 2009), the probability of males surviving beyond 10 years, after reaching one year of age, is likely lower. This suggests that the male age structure of the population may be skewed to younger animals with few males reaching full physical and behavioural maturity (Yoccoz et al. 2002, Bender et al. 2003), and is similar to the 0.1 probability of males reaching 4.5 years of age in a harvested Norwegian red deer population (Langvatn and Loison 1999). A skewed male age structure could have consequences for productivity of the population (Noyes et al. 1996, Milner et al. 2007).

We interpret the different recovery rates in Alberta and Saskatchewan as a result of the distinct regulatory requirements of each jurisdiction. While a cohort effect in survival could be expected (Rose et al. 1998), any potential mechanism(s) resulting in cohort-specific recovery rates are far less plausible than recovery rates influenced by hunting regulations. Given that regulatory requirements for elk hunters in Alberta were generally more stringent than in Saskatchewan and substantially more enforcement personnel and Park management staff were present in Alberta, the different recovery rates were not surprising. These two factors likely resulted in the recovery rate of Alberta captured animals being nearly twice as large as those captured in Saskatchewan. It is therefore conceivable that animal retrieval (c) and tag reporting (λ) rates were also higher in Alberta.

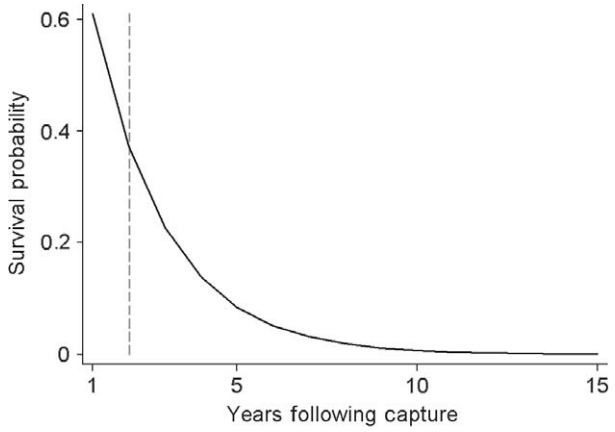


Figure 2. Cumulative survival probability of male elk in the Cypress Hills, Canada, to 15 years following capture. As all animals were captured at the same age, this also indicates the estimated survival probability to a future age after a male reached one year of age. The dashed vertical line represents the mean longevity following capture (2.02 years).

Given the strong enforcement presence it is plausible that λ and c both approached 1.0 in Alberta, making f a reasonable proxy for the true harvest rate, which is of direct interest for management (Vucetich et al. 2005). In particular, it is a reasonable assumption that reporting rates (λ) did approach 1.0, given the legally mandated reporting requirements for harvested elk in Alberta, while retrieval rates (c) of killed animals may be <1.0 (e.g. due to wounding loss). Reporting rates in Saskatchewan may be lower than those in Alberta due to reduced enforcement presence. Given the overall enforcement presence, the number of hunters in the area at any given time, wounding losses from other areas (Unsworth et al. 1993, Smith and Anderson 1998, McCorquodale et al. 2003), and our personal observations, $c<0.50$ for either Alberta or Saskatchewan was deemed unlikely.

Considering a range of values for c and λ in Saskatchewan, the predicted harvest rate rarely had the potential to exceed that of Alberta (Fig. 3). As both retrieval and tag reporting rates decrease, predicted harvest rates increase. Only when the Saskatchewan tag reporting rate was reduced to 0.6 could the Saskatchewan harvest rate potentially exceed that of Alberta. This may have been due to greater accessibility (e.g. roads and trails) for hunters in the Alberta portion of the Cypress Hills (Fig. 1) thus increasing male elk mortality risk (Leptich and Zager 1991). Additionally, hunting was prohibited in Fort Walsh National Historic Site, and from 1998–2001 there were large parcels of privately owned land bordering the southern edge of CHIP in Saskatchewan where elk hunting was not permitted, effectively creating a refuge. Further evidence suggesting both retrieval and/or tag reporting rates were lower in Saskatchewan is found in the natural mortality, and non-recovery, rates (m). The rate for Saskatchewan was particularly high compared to Alberta and

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

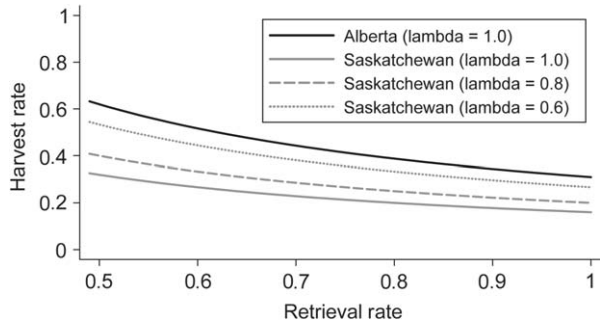


Figure 3. Predicted harvest rates ($K = f\lambda^{-1}c^{-1}$) of male elk in the Alberta (black) and Saskatchewan (gray) portions of the Cypress Hills, Canada, over a range (0.50–1.0) of retrieval rates (c) of killed animals. A tag reporting rate (lambda = λ) of 1.0 was assumed for Alberta, and for Saskatchewan three values of lambda are provided. Harvest rate was calculated using estimated recovery rates (f) of 0.31 and 0.16 for Alberta and Saskatchewan, respectively.

natural male mortality rates reported elsewhere including Kentucky ($m = 0.08$; Larkin et al. 2003), North Carolina ($m = 0.089$; Murrow et al. 2009), and Norway ($m = 0.06$; Loison and Langvatn 1998). It is difficult to identify a mechanism that would lead to a nearly four-fold increase in natural mortality in Saskatchewan males versus those in Alberta. The most plausible explanation lies in lower animal retrieval and/or tag reporting rates (i.e. the non-recovery component of m).

The difference in estimated recovery rates between Alberta and Saskatchewan is not trivial. Under certain assumptions, these rates can be used to gain a greater understanding of harvest pressures on elk in each jurisdiction. From an analytical perspective, modeling recovery rates separately for each jurisdiction does have an impact on the estimated survival rate in the population. For instance, if a model with constant recovery (i.e. f.) had been used (not shown) the estimated survival rate would have been 0.57. While this may not be significantly different from 0.61 from a statistical perspective, it may be biologically significant owing to the potential influence of this demographic parameter on population growth rate.

This research highlights the importance of considering regulatory regimes and requirements when investigating and interpreting demographic and population dynamics of populations managed across jurisdictions. Details of these requirements (e.g. mandated kill reporting) are necessary for developing reasonable inferences from analytical results, and hence for making informed management decisions. In the Cypress Hills, identifying these regulatory differences between Alberta and Saskatchewan enabled us to obtain better and likely more accurate information from harvest data. If we had ignored the differences between jurisdictions our understanding of the mechanisms resulting in differing recovery would have been weaker. Furthermore, accounting for these differences in a statistical framework influenced our estimated survival rate. Dependent on the magnitude of regulatory differences in other systems, their effect(s) on estimated vital rate parameters could be much more significant.

Acknowledgements – J. Skilnick and G. Chapman provided valuable field assistance during this work and a number of technicians provided assistance during animal capture efforts. Financial support for the project was provided by Alberta Environment and Alberta Sustainable Resource Development, Rocky Mountain Elk Foundation Canada, Alberta Conservation Association, University of Calgary, and the Alberta Sports, Recreation, Parks, and Wildlife Foundation. In-kind and logistical support was provided by Cypress Hills Interprovincial Park (Alberta) and Saskatchewan Environment. In particular D. Dobson, W. Harris, K. Redden, O. Tarnasky and L. Weekes provided support throughout the study and M. Lindberg provided statistical assistance. D. Gustine provided valuable comments on an earlier draft of this manuscript.

References

Anderson, D. R. et al. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. – J. Anim. Ecol. 54: 89–98.

Bender, L. C. and Miller, P. J. 1999. Effects of elk harvest strategy on bull demographics and herd composition. – Wildlife Soc. Bull. 27: 1032–1037.

Bender, L. C. et al. 2003. Body mass and antler development patterns of Rocky Mountain elk (*Cervus elaphus nelsoni*) in Michigan. – Am. Midl. Nat. 150: 169–180.

Biederbeck, H. H. et al. 2001. Effects of hunting regulations on bull elk survival and age structure. – Wildlife Soc. Bull. 29: 1271–1277.

Bolker, B. M. 2008. Ecological models and data in R. – Princeton Univ. Press.

Breitung, A. J. 1954. A botanical survey of the Cypress Hills. – Can. Field Nat. 68: 55–92.

Brownie, C. et al. 1985. Statistical inference from band-recovery data – a handbook, 2nd edn. – US Fish and Wildlife Service Resource Publ. 156, Washington, DC.

Buckland, S. T. et al. 1996. Estimating the minimum population size that allows a given annual number of mature red deer stags to be culled sustainably. – J. Appl. Ecol. 33: 118–130.

Bunnefeld, N. et al. 2011. Management strategy evaluation: a powerful tool for conservation? – Trends Ecol. Evol. 26: 441–447.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.

Caughley, G. 1977. Analysis of vertebrate populations. – Wiley.

Chee, Y. E. and Wintle, B. A. 2010. Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. – J. Appl. Ecol. 47: 1169–1178.

Connelly, J. W. et al. 2012. Harvest management. – In: Silvy, N. J. (ed.), The wildlife techniques manual: management, 7th edn. – The John Hopkins Univ. Press, pp. 202–231.

Coulson, T. et al. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. – J. Anim. Ecol. 74: 789–801.

Environment Canada 2000. Canadian daily climate data, Vol. 1.02. – Climate Information Branch, Atmospheric Environment Service, Environment Canada, Ottawa, ON, Canada.

Festa-Bianchet, M. 2012. The cost of trying: weak interspecific correlations among life-history components in male ungulates. – Can. J. Zool. 90: 1072–1085.

Gaillard, J.-M. et al. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. – Trends Ecol. Evol. 13: 58–63.

Gaillard, J.-M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores, – Annu. Rev. Ecol. Syst. 31: 367–393.

Garrott, R. A. et al. 2003. Climate-induced variation in vital rates of an unharvested large herbivore populations. – Can. J. Zool. 81: 33–45.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Gordon, I. J. et al. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. – J. Appl. Ecol. 41: 1021–1031.
Grøtan, V. et al. 2009. Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose. – Oecologia 161: 685–695.
Hegel, T. M. et al. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. – J. Environ. Manage. 90: 222–235.
Jorgenson, J. T. et al. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. – Ecology 78: 1019–1032.
Keith, R. C. 1977. A preliminary study of the winter ecology of elk in the Cypress Hills of Saskatchewan. – PhD thesis, Univ. of Regina, Regina, SK, Canada.
Kimball, J. F. and Wolfe, M. L. 1974. Population analysis of a northern Utah elk herd. – J. Wildlife Manage. 38: 161–174.
Langvatn, R. and Loison, A. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. – Wildlife Biol. 5: 213–223.
Larkin, J. L. et al. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. – J. Wildlife Manage. 67: 467–476.
Lebreton, J.-D. et al. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.
Leptich, D. J. and Zager, P. 1991. Road access management effects on elk mortality and population dynamics. – In: Christensen, A. G. et al. (eds), Proc. of elk vulnerability, a symposium. Montana State Univ., Bozeman, MT, USA, pp. 126–131.
Loison, A. and Langvatn, R. 1998. Short- and long-term effects of spring weather on growth and survival of red deer in Norway. – Oecologia 116: 489–500.
Loison, A. et al. 1999. Age-specific survival in five populations of ungulates: evidence of senescence. – Ecology 80: 2539–2554.
McCorquodale, S. M. et al. 2003. Survival and harvest vulnerability of elk in the Cascade Range of Washington. – J. Wildlife Manage. 67: 248–257.
McCorquodale, S. M. et al. 2011. Elk survival and mortality causes in the Blue Mountains of Washington. – J. Wildlife Manage. 75: 897–904.
Milner, J. M. et al. 2007. Demographic side effects of selective hunting in ungulates and carnivores. – Conserv. Biol. 21: 36–47.
Murrow, J. L. et al. 2009. Demographics of an experimentally released population of elk in Great Smoky Mountains National Park. – J. Wildlife Manage. 73: 1261–1268.
Mysterud, A. et al. 2002. The role of males in the dynamics of ungulate populations. – J. Anim. Ecol. 71: 907–915.
Nelson, L. J. et al. 1980. The effect of band loss on estimates of annual survival. – J. Field Ornithol. 51: 30–38.
Newsome, R. D. and Dix, R. L. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. – Am. Midl. Nat. 80: 118–185.
Noyes, J. H. et al. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. – J. Wildlife Manage. 60: 508–517.
Peek, J. M. et al. 1967. Population changes within the Gallatin elk herd, 1932–1965. – J. Wildlife Manage. 31: 304–316.
Pettorelli, N. et al. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. – Proc. R. Soc. B 269: 747–753.
Raedeke, K. J. et al. 2002. Population characteristics. – In: Toweill, D. E. and Thomas, J. W. (eds), North American elk: ecology and management. Smithsonian Inst. Press, Washington, DC, USA, pp. 449–491.
Rankin, D. J. and Kokko, H. 2007. Do males matter? The role of males in population dynamics. – Oikos 116: 335–348.
Redpath, S. M. et al. 2013. Understanding and managing conservation conflicts. – Trends Ecol. Evol. 28: 100–109.
Rose, K. E. et al. 1998. Cohort variation in male survival and lifetime breeding success in red deer. – J. Anim. Ecol. 67: 979–986.
Sauer, J. R. and Boyce, M. S. 1983: Density dependence and survival of elk in northwestern Wyoming. – J. Wildlife Manage. 47: 31–37.
Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edn. – Wiley.
Smith, B. L. 2001. Winter feeding of elk in western North America. – J. Wildlife Manage. 65: 173–190.
Smith, B. L. and Anderson, S. H. 1998. Juvenile survival and population regulation of the Jackson elk herd. – J. Wildlife Manage. 62: 1036–1045.
Soper, J. D. 1946. Mammals of the northern Great Plains along the international boundary in Canada. – J. Mamm. 27: 127–153.
Toïgo, C. and Gaillard, J.-M. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environmental harshness? – Oikos 101: 376–384.
Unsworth, J. W. et al. 1993. Elk mortality in the Clearwater drainage of northwest Idaho. – J. Wildlife Manage. 57: 495–502.
Vucetich, J. A. et al. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. – Oikos 111: 259–270.
White, G. C. 1985. Survival rates of wapiti (*Cervus elaphus nelsoni*) in the Jemez Mountains, New Mexico, USA. – R. Soc. N. Z. Bull. 22: 51–54.
White, G. C. and Burnham, K. P. 1999. Program MARK: survival rate estimation from both live and dead encounters. – Bird Study 46(Suppl.): S120–S139.
Widenmaier, K. J. and Strong, W. L. 2010. Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. – For. Ecol. Manage. 259: 1870–1879.
Williams, B. K. et al. 2001. Analysis and management of animal populations: modeling, estimation and decision-making. – Academic Press.
Yoccoz, N. G. et al. 2002. Age- and density-dependent reproductive effort in male red deer. – Proc. R. Soc. B 269: 1523–1528.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Appendix 1. Candidate models, and model selection results, of recovery (*f*) and survival (*S*) for male elk (n = 47) in the Cypress Hills, Canada (1998–2001).

Model[a]	No. of parameters	AICc	ΔAICc
$S.\ f_g$	3	115.98	0
$S_g\ f.$	3	117.55	1.57
$S.\ f.$	2	117.92	1.94
$S_g\ f_g$	4	118.37	2.39
$S_{Yr1}\ f_g$	4	118.37	2.39
$S.\ f_t$	4	118.41	2.43
$S_g\ f_{Yr1}$	4	119.94	3.96
$S_t\ f.$	4	120.06	4.08
$S.\ f_{Yr1}$	3	120.15	4.17
$S_{Yr1}\ f.$	3	120.15	4.17
$S_g\ f_t$	5	120.88	4.90
$S_t\ f_g$	5	120.88	4.90
$S_t\ f_{Yr1}$	5	122.27	6.29

[a] only those models that are numerically identifiable (Williams et al. 2001) are reported.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use