

FINAL ANNUAL REPORT

Grant #: 0226000010

**Elk Population Size Estimates in Kentucky during 2019–2022 from Statistical
Population Reconstruction Models**

Produced by:

Sean M. Murphy, Kathleen E. Williams, Matthew T. Springer, and John J. Cox

Department of Forestry and Natural Resources
University of Kentucky
105 T.P. Cooper Building
730 Rose Street
Lexington, KY 40546-0073

June 22, 2023

EXECUTIVE SUMMARY

Monitoring key population characteristics, such as population size, across time is critical for effective implementation of wildlife conservation and management actions. Such monitoring has increased importance for populations that were established using reintroduction, because reintroduced populations often have elevated risks of developing demographic and genetic anomalies. Elk (*Cervus canadensis*) were reintroduced to southeastern Kentucky during 1997–2002 and elk hunting was first implemented in 2001. The number of elk permits allotted to hunters has increased substantially since then, but uncertainty has remained about elk population size and trajectory. A recent genetic study found that elk in Kentucky constitute a genetically distinct population that is isolated, whereas other studies documented moderate demographic rates (e.g., survival, reproduction, etc.) over the last decade. Additionally, a recent study conducted by University of Montana researchers using statistical population reconstruction (SPR) models estimated the elk population in Kentucky was comprised of approximately 10,000 individuals by 2018. However, data availability and quality were limited for that analysis and, therefore, it was considered a proof-of-concept that showed SPR models could be used to estimate Kentucky elk population size but that refinements to data collection would be needed. Building on that analysis, biologists at Kentucky Department of Fish and Wildlife Resources and researchers at University of Kentucky collaboratively implemented large-scale changes to data collection beginning in 2019. In this report, we present the results of those data collection efforts and provide updated hunter effort, population size, population growth rate, survival, and mortality estimates for elk in Kentucky during 2019–2022. Across the 4-year study period, a total of 984 elk (622 Males; 362 Females) were legally harvested in the Elk Restoration Zone. The age structure of harvested elk was skewed towards young adults (median = 3.5–4.5 years), but calves, yearlings, and adults of both sexes were harvested. A total of 1,920 elk hunters answered hunting effort-related questions in the mandatory post-hunt surveys, which allowed us to determine that hunters with firearm permits expended the least amount of hunting effort (mean = 4–5 days), followed by archery permits (mean = 8–9 days) and other types of permits (youth, landowner, Commission, etc. permits; mean = 8–9 days). A total of 354 elk (109 Males; 245 Females) that represented calves, yearlings, and adults were live-captured and outfitted with radio-collars during 2019–2022. Among those radio-collared individuals, 126 elk (51 Males; 75 Females) died from harvest-related (48%) and non-harvest (52%) causes; substantial variation in mortality rates existed between sexes and among age classes within each sex across time. We integrated the age-at-harvest data, hunter effort data, and survival and mortality data in a suite of SPR models that we fit to estimate elk population sizes during 2019–2022. Point estimates of female elk abundance ranged from 3,884 to 7,361 females, whereas point estimates of male elk abundance ranged from 3,355 to 4,135 males. Total population size estimates ranged from 8,019 to 11,118 elk, with a final estimate for 2022 of 10,661 elk in Kentucky; those estimates corresponded to an average annual population growth rate of 1.10 (95% CI = 0.88–1.25) during 2019–2022. The results of this 4-year study demonstrate that the refinements in data collection that occurred provided a wealth of information from which a reliable trend in elk population sizes could be estimated with SPR models. We contend that SPR models and targeted data collection within that framework provides a robust approach for monitoring elk population trends into the future. Additionally, despite enduring isolation of the Kentucky elk population, the sustained trend of positive population growth has likely prevented development of deleterious demographic and genetic issues, which supports long-term reintroduction success.

INTRODUCTION

Obtaining reliable, contemporary estimates of key demographic parameters, such as population size and population growth rate, is critical for effective implementation of wildlife conservation and management actions. Monitoring demographic parameters across time has heightened importance for large mammals, particularly if populations are the product of reintroduction and are legally hunted. Large mammals typically occur at low population densities, have low reproductive rates, and exhibit slow population growth rates, all of which render them susceptible to catastrophic events and environmental stochasticity that can lead to severe population declines that are often unrecognized early in the process (Erb and Boyce 1999). Furthermore, reintroduced species that remain isolated for lengthy periods post-establishment risk developing deleterious demographic and genetic anomalies (Kanarek et al. 2015; Szucs et al. 2017). Consequently, large mammal population monitoring at regular intervals is critical for evaluating both short- and long-term reintroduction success, informing conservation and management actions, and implementing adaptive management strategies if issues arise (Robert et al. 2015; Murphy et al. 2015, 2016, 2019a,b).

During 1997–2002, a total of 1,547 elk (*Cervus canadensis*) were reintroduced to southeastern Kentucky to attempt to establish a viable population of an ecologically important but extirpated large mammal that historically inhabited the region (Larkin et al. 2001, Cox 2011). Early demographic monitoring indicated high post-release survival rates and increasing reproductive rates among the founder elk, despite few adult males being released, which suggested short-term reintroduction success (Larkin et al. 2003). In response to a presumed population increase, a limited elk hunt was first implemented in 2001, followed by an exponential increase and calibration of annual elk permits issued between 2004 and 2009, after which approximate equilibration of available permits has occurred (Kentucky Department of Fish and Wildlife Resources [KDFWR] 2016).

Results from a recent population genetics analysis indicated that the elk population in Kentucky has remained isolated long enough, and with very limited immigration from neighboring elk populations in eastern Tennessee, that elk in Kentucky represent a genetically distinct population (Muller et al. 2018). Additional studies of elk in Kentucky over the last decade indicated that adult elk survival rates in parts of southeastern Kentucky were moderate (Slabach et al. 2018) and adequate reproduction and calf survival continues to be documented (K.E. Williams, unpublished data). Further, results from statistical population reconstruction (SPR) models suggested that the elk population in Kentucky likely increased to approximately 10,000 individuals by 2018 (Millsbaugh and Clawson 2019; hereafter referred to as the ‘University of Montana Analysis’). Collectively, these findings suggested that the elk population in Kentucky was likely of large enough size with sufficient demographic rates to mitigate development of potential population-level genetic consequences that could be caused from the long-term isolation identified by Muller et al. (2018; also see Youngmann et al. [2020]).

As with other wild game species, continued demographic monitoring of elk in Kentucky will be needed to inform management, including possible adjustments to legal harvest structure, and to evaluate the effectiveness of management actions. Although the University of Montana Analysis produced the first robust and defensible population size estimates for elk in Kentucky, that analysis was a proof-of-concept designed to evaluate if SPR models could be used to reliably estimate elk population size in Kentucky into the future. The analysis ultimately concluded that SPR could be used, but it also identified multiple shortcomings in data

collection/availability and provided associated recommendations for improving the underlying Kentucky elk datasets used by SPR models to obtain more robust and precise population size estimates (Millspaugh and Clawson 2019).

Herein, we present: (1) results of SPR-specific elk research and data collection that occurred in Kentucky during 2019–2022, (2) updated elk population size estimates from SPR models, and (3) recommendations for continued elk demographic monitoring. The work presented in this report directly builds on the foundational University of Montana Analysis, which produced elk population size estimates in Kentucky for the period 2014–2018. Specifically, this report not only provides contemporary elk population size estimates that are critical to management of this ecologically, economically, and recreationally important large mammal, but also reflects the effectiveness of targeted changes in research and data collection methods that better align with the requirements and assumptions of SPR models.

METHODS

Statistical Population Reconstruction Data Requirements

SPR models were formally developed 20 years ago as an extension of virtual population analysis (VPA) models that were originally conceptualized for hindcasting (i.e., estimating past conditions) of fisheries stocks (Fry 1949, Gulland 1965, Gove et al. 2002). More conventional methods of population reconstruction, such as the Downing method (Downing 1980), rely on age-at-harvest data and rough independent approximations of survival, harvest, and harvest reporting rates, which prevent appropriate propagation of uncertainty to abundance estimates (Roseberry and Woolf 1991). Consequently, conventional reconstruction methods necessitate strong assumptions that large mammal populations and the structure of their harvests typically violate, leading to inaccurate and often volatile population size estimates (Davis et al. 2007). In contrast, SPR models employ joint likelihood methods to simultaneously estimate survival, harvest, and recruitment rates and population sizes in previous years, thereby representing a major improvement over conventional reconstruction models (Gove et al. 2002, Skalski et al. 2007, Gast et al. 2013).

Age-at-harvest Data

The foundational data required for all wildlife population reconstruction models, including conventional approaches and SPR, are annual counts of the number of individuals of a given age or age class within each sex that were legally harvested (i.e., sex-specific age-at-harvest data). Although age-at-harvest data are typically straightforward for state wildlife agencies to collect with little effort, the reliability of those data is sometimes questionable. For example, if harvest reporting by hunters is not mandatory, then the age- or age class-specific counts of harvested individuals within a given year may be underreported and cause bias in population size estimates (Gove et al. 2002).

Additionally, accurate classification of the sex and age or age class of each harvested individual is critical to generating reliable age-at-harvest datasets and, therefore, obtaining accurate population size estimates from SPR models (Gove et al. 2002; Skalski et al. 2007, 2012). However, methods used for determining the sex and age of harvested animals varies among species, with some methods having much greater accuracy than others. In general, jaw or tooth analyses (e.g., cementum annuli analysis) and genitalia extraction or genetic analyses are the most reliable aging and sexing methods, respectively, for most medium and large mammal

species. In contrast, visual examinations are the least reliable, regardless of whether hunters or trained biologists conduct those examinations, as both sets of individuals have been shown to inaccurately identify the sex and age of harvested animals of multiple species at alarmingly high rates (Williams et al. 2011, Gee et al. 2014, Beausoleil and Warheit 2015). For instance, Murphy et al. (2022) found that simply switching the sexing and aging protocol from the more accurate genitalia examinations and cementum annuli tooth analyses, respectively, to visual assessments conducted by hunters may have caused SPR models to overestimate bobcat (*Lynx rufus*) population sizes by nearly 100%.

Hunter Effort Data

Accounting for hunter effort is important for SPR models to accurately estimate harvest probabilities and therefore population sizes from harvest data (Clawson 2015). Harvest effort is often measured in number of tags or permits sold or number of hours or days spent hunting. The choice of which metric to use as a measure of hunter effort largely depends on the prescribed harvest structure; for instance, if the number of available tags/permits are limited, the harvest season is of short duration, and the hunter participation rate is high (at or near 100%), then the number of tags/permits sold might be a useful measure of hunter effort. However, in most cases, the time (hours or days) spent hunting or scouting + hunting is the most detailed and information-rich form of hunter effort that can and should be used in SPR models (Clawson et al. 2017).

Auxiliary Data

Unfortunately, even if the age and sex classifications of harvested individuals are accurate, the relatively easily collected age-at-harvest data alone are insufficient for estimating population size and differentiating among survival and harvest rate processes (Gove et al. 2002, Skalski et al. 2007). Therefore, auxiliary data are required for SPR models to reliably estimate survival rates, harvest rates, and population sizes (Clawson et al. 2013). The most commonly collected auxiliary data for harvested large mammal populations are time-to-event survival and mortality data from radio-collar deployment and monitoring (Hatter et al. 2018, Johnson et al. 2019, Howard et al. 2020). Other auxiliary data can also be useful; for example, obtaining an independent estimate of population size using capture-mark-recapture approaches in a single year can help calibrate the SPR model estimates of population size (Fieberg et al. 2010, Clawson et al. 2013, Gast et al. 2013).

Data Collection for SPR Modeling of Elk in Kentucky during 2019–2022

As noted previously, the University of Montana’s proof-of-concept SPR analysis conducted for elk in Kentucky identified multiple shortcomings of data availability and data collection methods that caused poorer than desirable estimate reliability (Millspaugh and Clawson 2019). Beginning in 2019, biologists at KDFWR and researchers at University of Kentucky (UK) collaboratively implemented the recommendations from the University of Montana Analysis to obtain data for producing more reliable elk population size estimates in Kentucky using SPR models.

Age-at-harvest Data

All sex-specific age-at-harvest data were collected by KDFWR biologists and staff via a combination of the Telecheck System, in-the-field examinations of harvested elk, and tooth-based aging via extraction and subsequent cementum annuli analysis conducted by Matson's Laboratory (Manhattan, MT). From those sources, sex-specific age-at-harvest matrices were constructed that contained the number of individuals in each of three age classes (calf: <1 year; yearling: 1 to <2 years; adult: ≥2 years) that were harvested during each year from the 2019–2020 season through the 2022–2023 season. Similar to the University of Montana Analysis, we chose to pool the harvest data into age classes rather than using actual ages because: 1) age was not determined via tooth cementum annuli analysis for all harvested elk; 2) harvest counts were very small for some actual ages; and 3) pooling to age class allowed our analysis and results to be directly comparable to those of the University of Montana Analysis.

Hunter Effort Data

All hunters who were drawn for and subsequently purchased an elk permit were required to complete a post-season hunt survey, regardless of whether their hunt was successful or not. Within the survey, hunters were asked to report the total number of days that they spent scouting prior to their hunt and the total number of days that they spent hunting. We used those hunter-reported scouting and hunting days to calculate permit type-specific hunter effort for each year.

Auxiliary Data

The University of Montana Analysis noted major deficiencies in the availability of auxiliary data for elk in Kentucky, which are required for fitting SPR models (Millsbaugh and Clawson 2019). Specifically, sample sizes of radio-collared elk were very small during some years, not all elk age classes were represented in the radio-collared sample during other years, and the geographical distribution of radio-collared elk during most years was confined to localized study areas instead of representing a scale-appropriate sample of the entire Elk Restoration Zone (e.g., Slabach et al. 2018, Hast 2019). Therefore, elk live-capture and radio-collar deployment efforts were substantially increased beginning in 2019 to address those shortcomings. This included an increase in the number of radio-collars deployed, the initiation of a multi-year calf survival study that facilitated monitoring of calves, and an expansion in the number and distribution of areas within the Elk Restoration Zone where radio-collars were deployed on elk.

Statistical Analyses of 2019–2022 Elk Monitoring Data

Hunter Effort

Based on the post-season hunter surveys, for each hunter within each year, we summed the reported number of days spent scouting with the reported number of days spent hunting and then divided the total number of days spent scouting + hunting by 10 to obtain hunter effort values on the 1.0 scale (i.e., hunter effort = $\frac{\text{Days Scouting} + \text{Days Hunting}}{10}$). This scaling ensured that all parameters were of similar magnitude, thereby improving stability of the SPR model numerical optimization process (Skalski et al. 2012). We fit a generalized linear model with Gamma error distribution and log link function to estimate permit type-specific hunter effort within each year (i.e., year × permit type fixed effects interaction; Ng and Cribbie [2017]). Additionally, we fit a separate generalized linear model with binomial error distribution (i.e., logistic regression) to estimate the permit type-specific probability of hunter success as a function of hunter effort. We

fit both models using the package *glmmTMB* in the R Statistical Computing Environment (Brooks et al. 2017, R Core Team 2023). We used the packages *ggeffects* and *emmeans* to obtain predicted marginal effects, standardized effect sizes, and respective 95% confidence intervals from the fitted models (Lüdtke 2018, Lenth 2023).

Auxiliary Survival and Mortality

Using the radio-collar monitoring data, we developed staggered-entry, right-censored, known-fate survival datasets. Radio-collared elk died from multiple causes (e.g., harvest, vehicle collisions, disease, etc. [Slabach et al. 2018]), but because SPR models only account for two broad types of mortality, harvest and non-harvest mortality, we collapsed all mortalities into those categories (Gast et al. 2013, Clawson et al. 2017). We then fit nonparametric Kaplan-Meier survival models using the R package *survival* to estimate sex \times age class-specific survival probabilities within each year (Pollock et al. 1989, Therneau and Grambsch 2000, Therneau 2023). Although better analytical approaches exist for estimating survival probabilities and quantifying the effects that biological and ecological factors may have on survival, such as Cox proportional hazards models (Murray and Patterson 2006), the assumptions of many of those models are incongruous with how survivorship is treated within the SPR framework (Gast et al. 2013, Clawson et al. 2017). In contrast, the Kaplan-Meier estimator is fully nonparametric and has fewer assumptions that are generally more easily satisfied.

However, it is reasonable to assume that elk mortality from harvest versus non-harvest sources represents a competing risks paradigm. In other words, harvest and non-harvest mortality sources are ‘competing’ to kill elk, such that the probability of an elk dying from harvest is at least partially dependent on the probability of that elk dying or not from a non-harvest mortality source (Heisey and Patterson 2006, Wolkewitz et al. 2014). The primary ramification of not accounting for multiple sources of mortality that are competing is that the Kaplan-Meier estimator may produce biased survival estimates (Southern et al. 2006). Using cumulative incidence functions (CIFs) to estimate competing cause-specific mortality probabilities is the optimal solution to this issue (Heisey and Patterson 2006, Wolkewitz et al. 2014). Therefore, we estimated CIFs using the R package *cmprsk* and obtained sex \times age class-specific probabilities of harvest and non-harvest mortality within each year (Gray 2022).

An important distinction between the formulation of survival probability based on CIFs and the formulation within SPR models is that, when harvest and non-harvest mortality processes are concurrent, the probabilities from CIFs are additive (e.g., $\text{Survival}_{\text{CIF}} = 1 - \text{Mortality}_{\text{Harvest}} - \text{Mortality}_{\text{Non-harvest}}$). In contrast, SPR models typically treat harvest and non-harvest mortality as conditionally independent (Gast et al. 2013, Clawson et al. 2017), such that survival probability is multiplicative (e.g., $\text{Survival} = [1 - \text{Mortality}_{\text{Harvest}}] \times [1 - \text{Mortality}_{\text{Non-harvest}}]$). Thus, to obtain non-harvest mortality probabilities, and therefore overall survival probabilities, that accounted for competing risks and also matched the multiplicative treatment of survival in SPR models, we corrected the estimated CIFs for non-harvest mortality using the equation described by Howard et al. (2020): $\text{Mortality}_{\text{Non-harvest}(\text{Corrected})} = 1 - \frac{(1 - \text{Mortality}_{\text{Harvest}} - \text{Mortality}_{\text{Non-harvest}})}{1 - \text{Mortality}_{\text{Harvest}}}$. By correcting the non-harvest mortality probabilities using this method, the corresponding survival probabilities match the SPR model formulation of survival: $\text{Survival}_{\text{CIF}} = (1 - \text{Mortality}_{\text{Harvest}}) \times (1 - \text{Mortality}_{\text{Non-harvest}(\text{Corrected})}$.

Population Size and Growth Rate

We integrated the annual age-at-harvest data, hunter effort estimates, and auxiliary survival and mortality probabilities to estimate elk population sizes during 2019–2022 using sex-specific SPR models fitted in a maximum likelihood framework (Gast et al. 2013, Clawson et al. 2017). For each sex, we fit models that varied by whether the auxiliary data used were age class-specific survival probabilities or mortality probabilities, and whether random effects for survival or harvest vulnerability were excluded or included to disregard or account for variation among years, respectively (Gast et al. 2013, Clawson et al. 2017, Howard et al. 2020). Additionally, we attempted to fit both method (permit type)-specific (i.e., firearm, archery, other) and period-specific (e.g., bull firearm week 1 versus week 2) SPR models for each sex that also included the aforementioned treatments of auxiliary data and random effects. After multiple attempts to fit SPR models with solely the 2019–2022 age-at-harvest data, we arrived at the realization that 4 years of age-at-harvest data were insufficient for obtaining reliable abundance estimates; therefore, we included the 2018 age-at-harvest data in all female- and male-specific SPR models (Millsbaugh and Clawson 2019). In all models, we accounted for the fact that not all elk were aged, whether based on cementum annuli analysis of teeth or visual examination by KDFWR biologists, by specifying a year-specific aging proportion effect (Clawson et al. 2017, Howard et al. 2020). We fit models using AD Model Builder via PopRecon 2.0 (Fournier et al. 2012, Clawson et al. 2017) and we used Akaike’s Information Criterion (AIC) for model ranking and selection; we produced estimates from the sex-specific models with the lowest AIC values (i.e., top-ranked model; Burnham and Anderson [2002], Skalski et al. [2012]).

We estimated an average annual population growth rate (λ_{Avg}) with the exponential growth equation (Gotelli 2008), which has been used for multiple other reintroduced populations of large mammals, including elk (Popp et al. 2014; Murphy et al. 2015, 2016; Louw et al. 2022). Although some individual elk herds in eastern Kentucky may exhibit logistic population growth that is regulated by ecological carrying capacity in a few localized areas, limited evidence exists to confirm this. Furthermore, considering the availability of potentially suitable but not yet occupied elk habitats throughout the entire Elk Restoration Zone (Hast 2019), it is reasonable to assume that exponential growth remains a more accurate characterization at the broader population level (Popp et al. 2014).

RESULTS

Data Collection for SPR Modeling of Elk in Kentucky during 2019–2022

Age-at-harvest Data

A total of 984 elk (622 Males; 362 Females) were legally harvested in the Elk Restoration Zone from the 2019–2020 season through the 2022–2023 season, resulting in a harvest sex ratio of 0.63M:0.37F. Actual ages based on cementum annuli analysis of extracted teeth were available for 243 males (39%) and 88 females (24%) that were harvested during the 4-year period. The youngest harvested elk of both sexes were 0.5 years-old, whereas the oldest harvested males and females were 12.5 and 16.5 years-old, respectively. Based solely on tooth ages, the age structures of both sexes across the entire 4-year span were skewed towards young adults ($\text{median}_{\text{Female}} = 3.5$; $\text{median}_{\text{Male}} = 4.5$; Fig. 1).

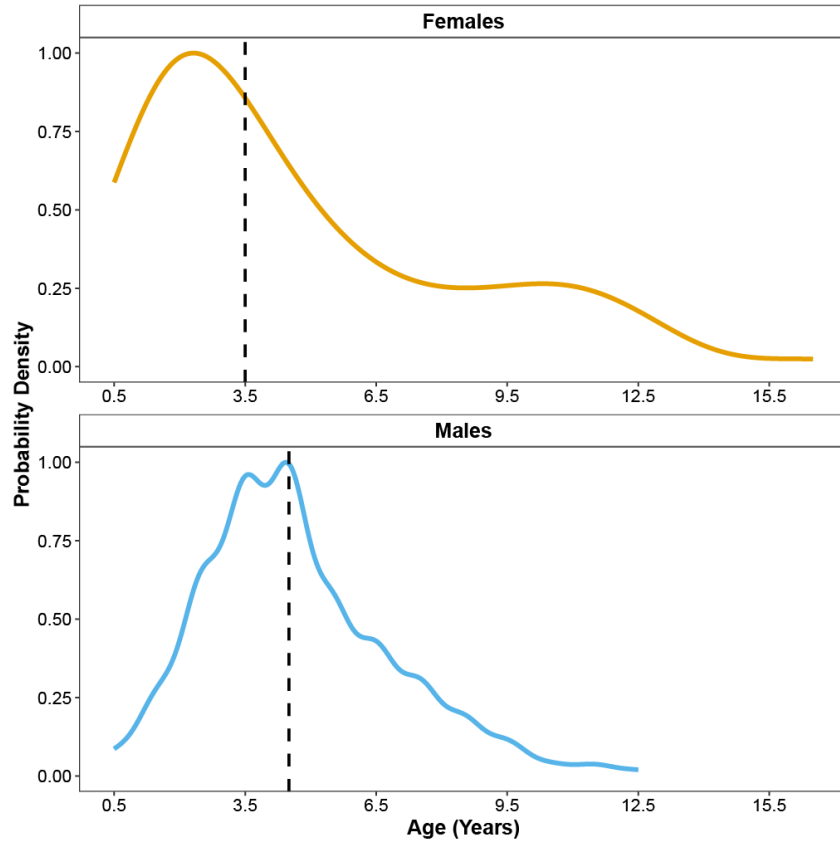


Figure 1. Age distributions based on cementum annuli analysis of teeth extracted from female ($n = 88$) and male ($n = 243$) elk that were legally harvested in Kentucky during 2019–2022. Median ages for each sex are denoted by the vertical black dashed lines; the median was used as the descriptive measure because the age distributions were right-skewed.

Based on the combination of cementum annuli analysis of extracted teeth and field-aging by KDFWR staff, the age structure of harvested elk was heavily skewed towards adults (Table 1): most harvested males were adults (87%; $n = 539$), followed by yearlings (10%; $n = 61$) and calves (3%; $n = 22$), and most harvested females were adults (91%; $n = 329$), followed by yearlings (7%; $n = 26$) and calves (2%; $n = 7$).

Table 1. Number of elk in each sex-specific age class that were legally harvested in Kentucky during 2019–2022. Ages are based on a combination of cementum annuli analysis of extracted teeth and field-aging conducted by KDFWR staff.

Year	Female Harvest			Male Harvest		
	Calves	Yearlings	Adults	Calves	Yearlings	Adults
2019	2	6	92	7	12	123
2020	2	5	78	4	16	164
2021	2	6	86	5	9	141
2022	1	9	73	6	28	107

Hunter Effort Data

A total of 1,920 elk hunters (98% of all hunters who completed post-hunt surveys) answered the post-hunt survey questions regarding the total number of days spent scouting and spent hunting during 2019–2022. A total of 1,715 of those hunters used their permits to hunt elk (89%), of which 795 hunters had successful hunts and harvested elk (46%). Collectively, most hunters who were drawn for permits purchased the permits and hunted, most hunters answered the effort questions on the post-hunt survey, and their responses reflected an approximately equal distribution of hunters who did and did not kill elk. Thus, the underlying data used to produce hunter effort estimates was likely unbiased; in other words, hunters who harvested an elk were not significantly more or less likely to answer the effort questions than hunters who did not harvest an elk.

Auxiliary Data

A total of 354 resident elk that represented both sexes and all age classes were live-captured, radio-collared, and had survival monitored during the 2019-20 season through the 2022-23 season. Among the 109 male elk that were monitored, 52, 15, and 42 individuals were first captured as adults, yearlings, and calves, respectively. Among the 245 female elk that were monitored, 175, 31, and 39 individuals were first captured as adults, yearlings, and calves, respectively. No calves or yearlings of either sex were radio-collared during 2019, but all age classes of both sexes were represented in the survival data for subsequent years.

Across all age classes, a total of 126 radio-collared elk (51 Males; 75 Females) died between January 2019 and January 2023 (i.e., end of the 2022-23 elk hunting season), which represented 36% of all elk that were radio-collared. Most male and female mortalities were adults ($n_{\text{Male}} = 34$; $n_{\text{Female}} = 62$), followed by calves ($n_{\text{Male}} = 12$; $n_{\text{Female}} = 7$) and yearlings ($n_{\text{Male}} = 5$; $n_{\text{Female}} = 6$). Causes of death included legal harvest ($n = 58$; 46%), unidentified/unknown ($n = 29$; 23%), predation ($n = 8$; 6%), disease and other natural factors ($n = 7$; 6%), capture myopathy ($n = 7$; 6%), agency euthanasia ($n = 7$; 6%), vehicle collision ($n = 4$; 3%), trauma ($n = 4$; 3%), and wounding loss by hunters ($n = 2$; 1%). Thus, 48% of elk died from harvest-related causes, whereas 52% of elk died from non-harvest causes, which was a nominal discrepancy not significantly different from an expected equal ratio ($\chi^2_1 = 0.14$; $p = 0.71$).

Statistical Analyses of 2019–2022 Elk Monitoring Data

Hunter Effort

Results from the generalized linear negative binomial model indicated substantial discrepancies in hunting effort between hunters who had firearm permits and hunters who had archery or youth/landowner/Commission permits (Fig. 2A). In general, hunters with cow elk firearm permits expended the least amount of hunting effort, with an average of 4.22 days (95% CI = 3.98–4.46) spent scouting + hunting per hunter across the 4-year period. In contrast, hunters with archery permits or youth/landowner/Commission permits expended the most amount of hunting effort, with an average of 8.81 days (95% CI = 8.57–9.04) and 8.62 days (95% CI = 8.21–9.03), respectively, spent scouting + hunting per hunter across the 4-year period. These estimated differences between hunters with firearm permits and all other permit types were statistically and biologically significant, with small p -values and small but non-negligible standardized effect sizes ($p < 0.0001$; $d = 0.15$ – 0.28). Ignoring the permit type (i.e., pooling hunter effort among permit types) resulted in nominal differences in average hunter effort

expended among years, with average hunter effort ranging from 5.99 days (95% CI = 6.07–6.99) during 2022 to 6.51 days (95% CI = 5.57–6.44) during 2021 (Fig. 2B).

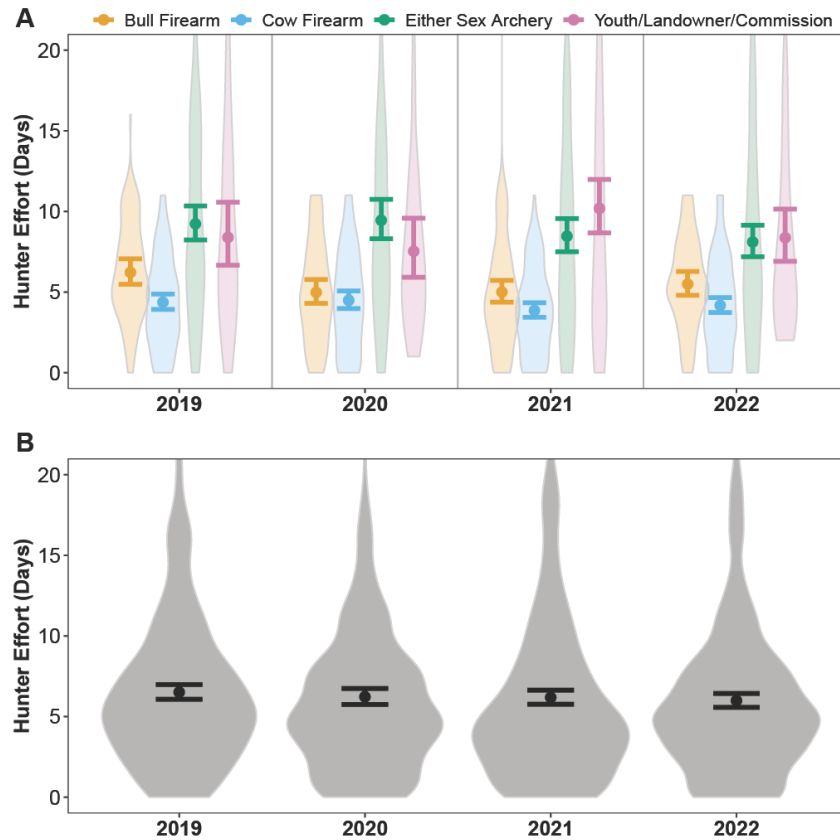


Figure 2. Predicted mean marginal effect estimates of elk hunter effort (days spent scouting + hunting) in Kentucky during 2019–2022 from a generalized linear model with negative-binomial error distribution. **A)** Mean hunter effort estimates by permit type among years; **B)** Mean hunter effort estimates among years after pooling permit types. Point estimates, 95% confidence intervals, and distributions of the raw data are represented by dots, error bars, and background violins, respectively.

Results from the generalized linear model with binomial error distribution (i.e., logistic regression) indicated that, for all permit types except archery permits, the probability of successfully harvesting an elk decreased with increasing hunter effort (Fig. 3A). Hunters with youth/landowner/Commission tags had the highest probability of successful elk harvest ($P_{(0-2 \text{ Days})} = 0.78$), which remained >0.50 out to 20 days of effort. Hunters with bull firearm permits had the next highest probability of successful elk harvest ($P_{(0-2 \text{ Days})} = 0.63$), which remained ≥ 0.50 out to 4 days of effort. Although hunters with cow firearm permits had lower probabilities of successful harvest than hunters with bull firearm permits, the relationship with hunter effort was similar for both bull and cow firearm permit hunters. In contrast, hunters with archery permits had a stable but relatively low probability of successful elk harvest ($P = 0.30-0.36$) that was uninfluenced by the amount of effort expended. Irrespective of permit type (i.e., pooling hunter effort among permit types), hunters who expended 1–4 days of hunting effort had the highest probabilities of successfully harvesting an elk (Fig. 3B).

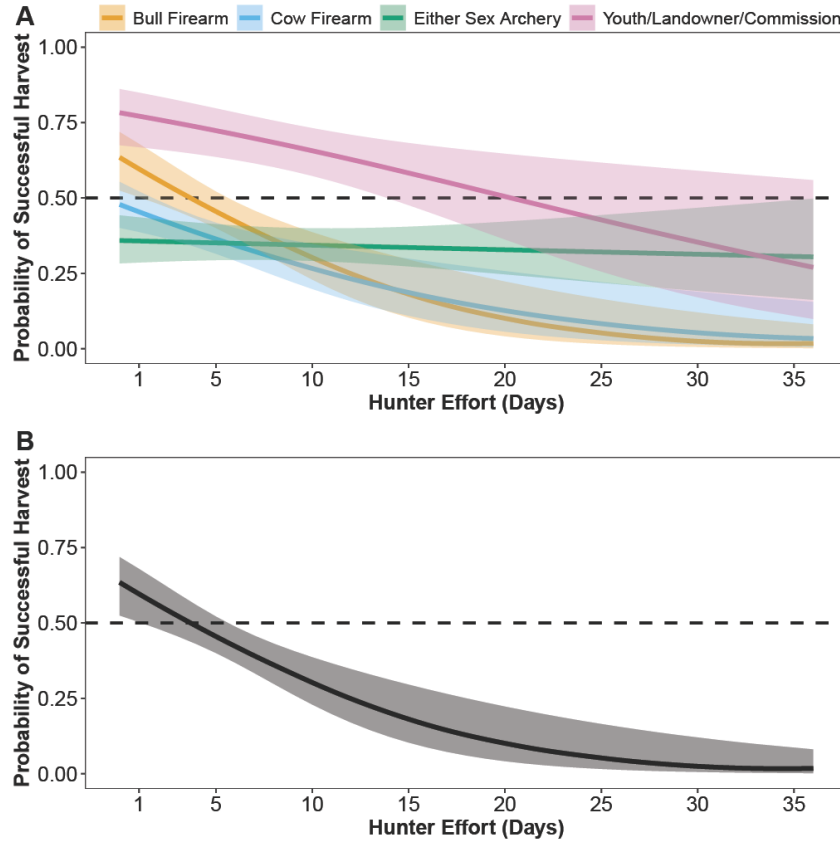


Figure 3. Predicted probabilities of successful elk harvest in Kentucky during 2019–2022 as a function of hunter effort (days spent scouting + hunting) for **A**) each elk permit type and **B**) permit types pooled together, based on post-season surveys completed by elk hunters. Colored lines and associated shaded regions denote point estimates and their 95% confidence intervals, respectively; horizontal dashed black line denotes the $P = 0.50$ threshold.

Auxiliary Survival and Mortality

Corrected estimates of non-harvest mortality probabilities ($M_{\text{CIF}[\text{Corrected}]}$) that were derived from probabilities estimated by cumulative incidence functions (M_{CIF}), all of which accounted for competing risks, differed by an average of 16% (range: 0–82%; Table 2). Most of the discrepancy between raw and corrected CIF estimates occurred for adult males.

Table 2. Non-harvest mortality probabilities for each sex and age class of radio-collared elk in Kentucky during 2019–2022, based on cumulative incidence functions (CIF) that accounted for competing risks. Columns convey raw CIF probabilities versus corrected probabilities (CIF_{Cor}).

Year	Females						Males					
	Calves		Yearlings		Adults		Calves		Yearlings		Adults	
	CIF	CIF _{Cor}	CIF	CIF _{Cor}	CIF	CIF _{Cor}	CIF	CIF _{Cor}	CIF	CIF _{Cor}	CIF	CIF _{Cor}
2019	–	–	–	–	0.07	0.08	–	–	–	–	0.13	0.17
2020	0.20	0.22	0.00	0.00	0.09	0.09	0.09	0.09	0.00	0.00	0.05	0.11
2021	0.35	0.35	0.00	0.00	0.17	0.20	0.50	0.50	0.20	0.27	0.13	0.31
2022	0.22	0.22	0.18	0.18	0.11	0.12	0.41	0.41	0.00	0.00	0.06	0.10

In general, estimated mortality probabilities reflected variation for female elk among age classes, whereas variation across time within each age class was nominal (Fig. 4A). Harvest had the highest mortality probability for yearling females ($M_{CIF} = 0.00\text{--}0.25$), non-harvest causes had the highest mortality probability for female calves ($M_{CIF[Corrected]} = 0.22\text{--}0.35$), but female adults had similar mortality probabilities for harvest and non-harvest causes ($M_{CIF[Corrected]} = 0.05\text{--}0.20$). In contrast, mortality probability estimates for male elk reflected substantial variation among age classes and across time within age classes (Fig. 4B). In general, harvest had the highest mortality probabilities for adult males ($M_{CIF} = 0.25\text{--}0.58$) and yearling males ($M_{CIF} = 0.17\text{--}0.67$), whereas non-harvest causes had the highest mortality probability for male calves ($M_{CIF[Corrected]} = 0.09\text{--}0.50$).

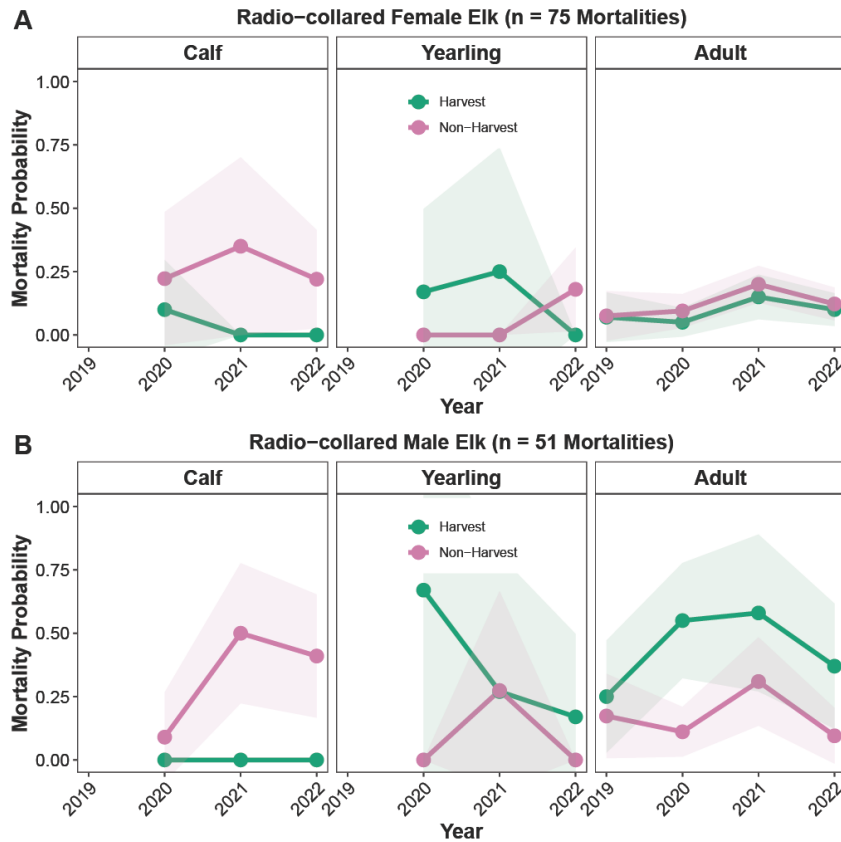


Figure 4. Point estimates of harvest and non-harvest mortality probability for all age classes of radio-collared **A)** female and **B)** male elk in Kentucky during 2019–2022, based on competing risks analysis using cumulative incidence functions and corrected to the multiplicative form that SPR models use (Howard et al. 2020). Background shaded regions represent 95% confidence intervals.

Derived multiplicative survival probabilities (S_{CIF}) based on corrected M_{CIF} estimates nominally differed from Kaplan-Meier estimated additive survival probabilities (S_{KM}) by $<1\%$. For female elk, annual S_{CIF} exhibited less pronounced variation across time within each age class, but differences among age classes existed (Fig. 4A); in general, calves had the lowest survival probabilities ($S_{CIF} = 0.65\text{--}0.78$), followed by yearlings ($S_{CIF} = 0.75\text{--}0.83$) and adults ($S_{CIF} = 0.68\text{--}0.86$). For male elk, annual S_{CIF} differed substantially among age classes and across time (Fig. 4B), such that adults generally had the lowest survival probabilities within each year ($S_{CIF} = 0.29\text{--}0.62$), followed by yearlings ($S_{CIF} = 0.33\text{--}0.83$) and calves ($S_{CIF} = 0.50\text{--}0.91$).

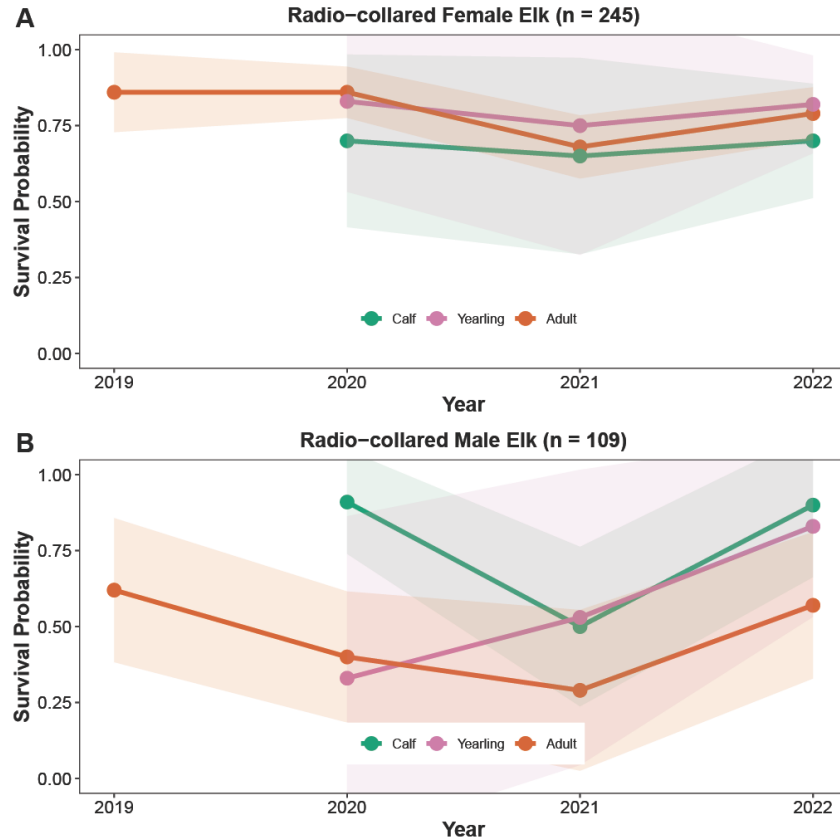


Figure 5. Point estimates of survival probability for all age classes of radio-collared **A)** female and **B)** male elk in Kentucky during 2019–2022, based on competing risks analysis using cumulative incidence functions and corrected to the multiplicative form that SPR models use (Howard et al. 2020). Background shaded regions represent 95% confidence intervals.

Population Size and Growth

Annual sample sizes for female elk that were harvested by the various permit types were too small for fitting method (permit)-specific SPR models, even if combined across permit types (Millspaugh et al. 2018; Table 3). Additionally, sample sizes within a harvest period (e.g., cow firearm week 1 versus cow firearm week 2) were too small for fitting period-specific SPR models. Therefore, we combined all female age-at-harvest data (i.e., pooled across methods and periods) and fit female models that considered four different hunter effort estimates: 1) cow firearm; 2) archery; 3) youth/landowner/Commission/etc.; and 4) the averages among 1–3. Combined with the different treatments of auxiliary data and random effects described in the Methods, this resulted in 16 total SPR models that we fitted to estimate female abundances.

Annual sample sizes for male elk that were harvested within a period (e.g., bull firearm week 1 versus bull firearm week 2) were also too small for fitting period-specific SPR models (Table 3). However, sample sizes combined across periods were sufficient for fitting method-specific male SPR models for firearm and archery seasons, but possibly not other seasons. To facilitate this, we pooled the bull firearm week 1 and week 2 data as ‘Male Firearm’, the archery/crossbow data as ‘Male Archery’, and the youth/landowner/Commission/etc. data as ‘Male Other’, then specified the corresponding method-specific hunter effort estimates in the associated SPR models. We also fit combined method models in which all male harvest data were pooled across methods and averaged year-specific hunter effort estimates were used. Thus,

combined with the different treatments of auxiliary data and random effects described in the Methods, we fit a total of 16 SPR models to estimate male elk abundances.

Table 3. Sex-specific elk harvest results in Kentucky by permit type during 2019–2022. The Other permit type represents the combination of youth, landowner, Commission, voucher, etc. permits. Asterisks (*) denote males that were harvested during cow firearm permit periods.

2019–2020 Season				
Permit	Female	Male Adult	Male Yearling	Male Calf
Firearm – Week 1	43	27	3	2*
Firearm – Week 2	39	21	2	2*
Archery/Crossbow	13	32	1	2
Other	5	44	5	1
2020–2021 Season				
Permit	Female	Male Adult	Male Yearling	Male Calf
Firearm – Week 1	33	39	4*	1*
Firearm – Week 2	37	35	2	3*
Archery/Crossbow	9	44	5	0
Other	6	48	3	0
2021–2022 Season				
Permit	Female	Male Adult	Male Yearling	Male Calf
Firearm – Week 1	44	29	0	1*
Firearm – Week 2	33	24	3	2*
Archery/Crossbow	12	40	5	2
Other	5	48	1	0
2022–2023 Season				
Permit	Female	Male Adult	Male Yearling	Male Calf
Firearm – Week 1	28	14	7	2*
Firearm – Week 2	39	26	6	2*
Archery/Crossbow	10	21	9	2
Other	6	46	6	0

Female elk abundance – For each measure of hunter effort considered, the top-ranked SPR model included mortality probabilities estimated from CIF_{Cor} as the auxiliary data and random effects that allowed interannual variation in mortality probabilities (Table 4). All other candidate models had $\Delta AIC > 7.00$ and were therefore beyond the range of AIC values within which models are typically considered competing (i.e., $\Delta AIC \leq 7.00$; Burnham and Anderson 2002, Burnham et al. 2011). Temporal trends in female abundance based on those 4 top-ranked models were similar, and nominal discrepancies existed depending on which measure of hunter effort was specified; for example, the 2022 female abundance estimates from the 4 models differed by only 0.21–1.71% ($range_{[2022]} = 6,483\text{--}6,595$ female elk). Therefore, because we did not know which estimate of hunter effort most accurately described the pooled female age-at-harvest data, we averaged point estimates among all 4 top-ranked models to produce final female elk abundance estimates. Final averaged estimates ranged from a low of 3,884 females (95% CI = 1,489–6,279) during 2019 to a high of 7,361 females (95% CI = 2,385–12,337) during 2021 (Table 5; Fig. 6).

Table 4. Model selection results for 16 fitted SPR models that were considered for estimating female elk abundance in Kentucky during 2019–2022. Models differed by which measure of hunter effort was specified, whether age-specific survival or mortality probability estimates were used as auxiliary data, and whether random effects were specified to allow interannual variation in age-specific survival or mortality probabilities. Annual estimates from models with the lowest AIC value within each group of hunter effort models were averaged to produce final female elk abundance estimates.

Hunter Effort	Model #	Auxiliary Data	Random Effects	K^a	LL ^b	AIC ^c	Δ AIC ^d
Firearm	1	Mortality	Yes	12	-49.55	123.10	0.00
	2	Mortality	No	11	-54.14	130.29	7.19
	3	Survival	Yes	12	-53.28	130.55	7.45
	4	Survival	No	11	-60.59	143.20	20.10
Archery	1	Mortality	Yes	12	-49.69	123.37	0.00
	2	Mortality	No	11	-54.28	130.56	7.19
	3	Survival	Yes	12	-53.39	130.78	7.41
	4	Survival	No	11	-60.70	143.40	20.03
Other	1	Mortality	Yes	12	-49.57	123.14	0.00
	2	Mortality	No	11	-54.16	130.32	7.18
	3	Survival	Yes	12	-53.38	130.76	7.62
	4	Survival	No	11	-60.68	143.36	20.22
Average	1	Mortality	Yes	12	-49.66	123.31	0.00
	2	Mortality	No	11	-54.25	130.50	7.19
	3	Survival	Yes	12	-53.56	131.11	7.80
	4	Survival	No	11	-60.86	143.71	20.40

^aNumber of model parameters; ^blog-likelihood of model; ^cAkaike’s Information Criterion of model; ^dDifference between AIC of model and AIC of top-ranked model.

Table 5. Point estimates of abundance, 95% confidence intervals (CI), and coefficient of variation (CV; estimate precision) for female elk in Kentucky during 2019–2022.

Year	Estimate (# Females)	95% CI	CV
2019	3,884	1,489–6,279	0.31
2020	6,277	1,455–11,099	0.39
2021	7,361	2,385–12,337	0.34
2022	6,543	2,711–10,375	0.30

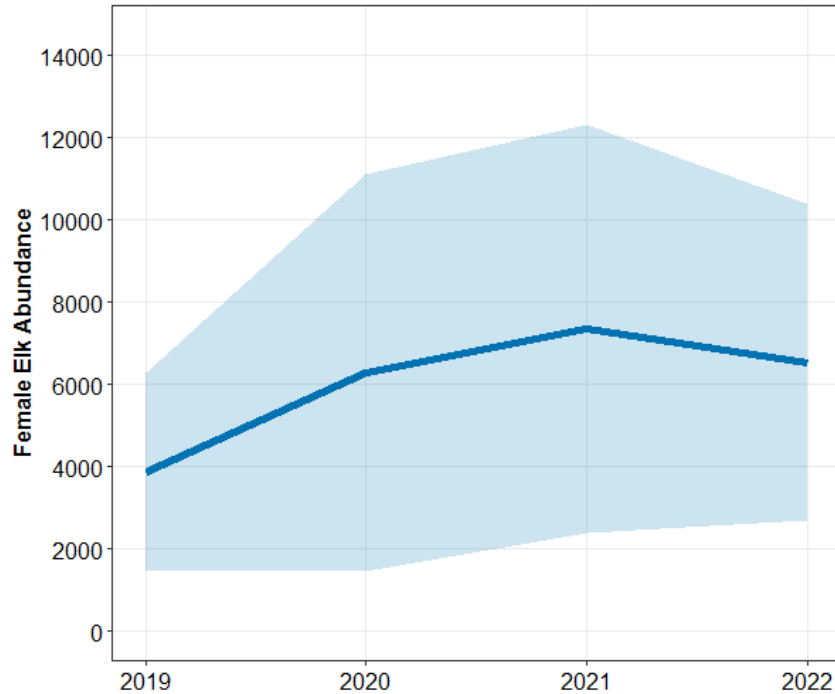


Figure 6. Point estimates (solid lines) and 95% confidence intervals (shaded regions) of female elk abundance in Kentucky during 2019–2022 from top-ranked SPR models.

Male elk abundance – The method-specific male models for firearm and archery permits converged and produced plausible estimates; however, the models for the other types of permits (e.g., youth, landowner, Commission, etc.) did not converge (Table 6). Convergence issues for those latter models were likely a consequence of small sample size, because no or few male calves or yearlings were harvested with youth, landowner, Commission, etc. permits. Unfortunately, because the models for the other types of permits did not converge, we could not combine method-specific abundance estimates to produce total male abundance estimates. Therefore, we produced male abundance estimates from the models in which all male harvest data were pooled across methods (permit types).

Similar to the female elk SPR models, the model that included mortality probabilities estimated from CIF_{Cor} as the auxiliary data and random effects that allowed interannual variation in mortality probabilities was the top-ranked model for male elk. Final estimates from this model ranged from a low of 3,355 males (95% CI = 772–5,938) during 2020 to a high of 4,135 males (95% CI = 713–7,557) during 2019 (Table 7; Fig. 7).

Table 6. Model selection results for 16 fitted SPR models that were considered for estimating male elk abundance in Kentucky during 2019–2022. Models differed by which method-specific age-at-harvest data (i.e., permit type) and corresponding hunter effort estimates were used, whether age-specific survival or mortality probability estimates were used as auxiliary data, and whether random effects were specified to allow interannual variation in age-specific survival or mortality probabilities.

Permit Type	Model #	Auxiliary Data	Random Effects	K^a	LL ^b	AIC ^c	ΔAIC^d
Firearm	1	Mortality	Yes	12	-55.65	135.30	0.00
	2	Mortality	No	11	-61.74	145.48	10.18
	3	Survival	Yes	12	-66.04	156.07	20.77
	4	Survival	No	11	-72.06	166.12	30.82
Archery	1	Mortality	Yes	12	-34.11	92.23	0.00
	2	Mortality	No	11	-38.75	99.49	7.26
	3	Survival	Yes	12	-42.89	109.79	17.56
	4	Survival	No	11	-49.93	121.86	29.63
Other	1	Mortality	Yes	12	Did not converge.		
	2	Mortality	No	11	Did not converge.		
	3	Survival	Yes	12	Did not converge.		
	4	Survival	No	11	Did not converge.		
Pooled	1	Mortality	Yes	12	-61.37	146.74	0.00
	2	Mortality	No	11	-66.06	154.11	7.37
	3	Survival	Yes	12	-69.93	163.87	17.13
	4	Survival	No	11	-76.78	175.56	28.82

^aNumber of model parameters; ^blog-likelihood of model; ^cAkaike’s Information Criterion of model; ^dDifference between AIC of model and AIC of top-ranked model.

Table 7. Point estimates of abundance, 95% confidence intervals (CI), and coefficient of variation (CV; estimate precision) for male elk in Kentucky during 2019–2022.

Year	Estimate (# Males)	95% CI	CV
2019	4,135	713–7,557	0.42
2020	3,355	772–5,938	0.39
2021	3,757	707–6,807	0.41
2022	4,118	655–7,581	0.43

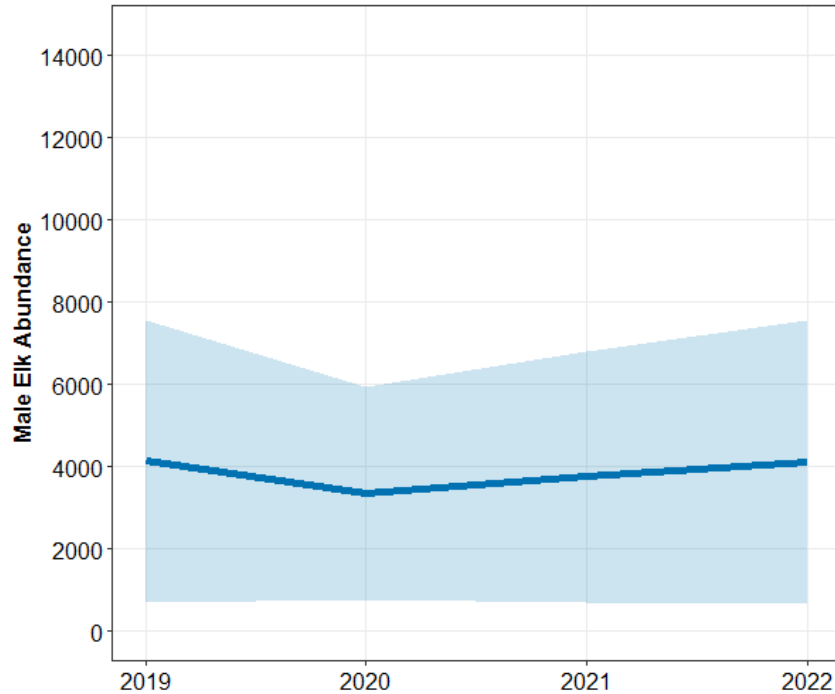


Figure 7. Point estimates (solid lines) and 95% confidence intervals (shaded regions) of male elk abundance in Kentucky during 2019–2022 from the top-ranked SPR model.

Combining the male and female estimates from the top-ranked SPR models resulted in total population size estimates that ranged from 8,019 elk (95% CI = 3,842–12,196) during 2019 to 11,118 elk (95% CI = 5,281–16,955) elk during 2021 (Table 8; Fig. 8). The final population size estimate for 2022 was 10,661 elk (95% CI = 5,496–15,826). Estimate precision, measured as coefficient of variation, ranged from 0.25 to 0.29, or an average of 0.27 across the 4-year period. Total elk population estimates corresponded to an average annual exponential population growth rate of $\lambda = 1.10$ (95% CI = 0.88–1.25) during 2019–2022.

Table 8. Point estimates of abundance, 95% confidence intervals (CI), and coefficient of variation (CV; estimate precision) for the elk population in Kentucky during 2019–2022.

Year	Estimate (# Elk)	95% CI	CV
2019	8,019	3,842–12,196	0.27
2020	9,632	4,162–15,102	0.29
2021	11,118	5,281–16,955	0.27
2022	10,661	5,496–15,826	0.25

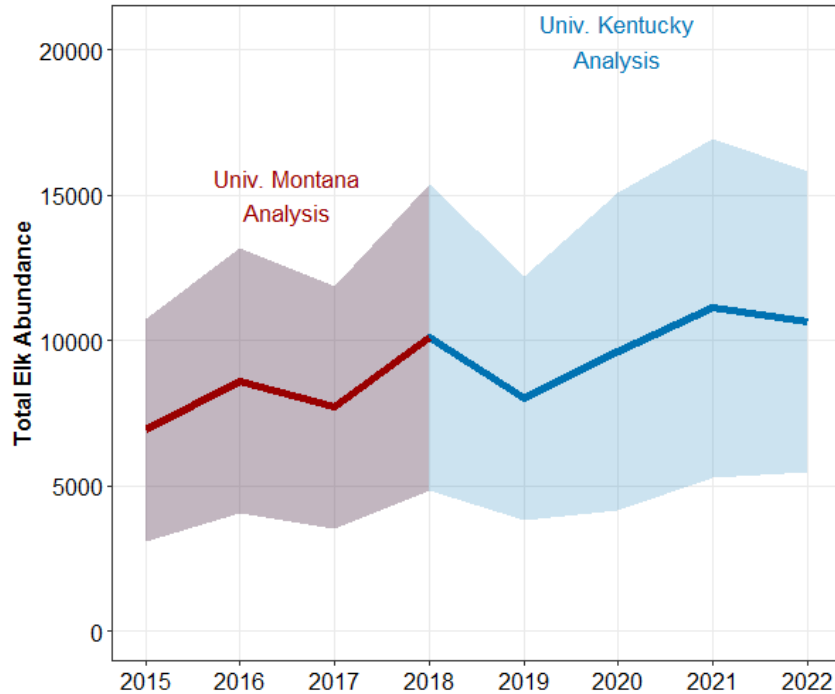


Figure 8. Point estimates (solid lines) and 95% confidence intervals (shaded regions) of total elk abundance in Kentucky during 2015–2022 from SPR models. Estimates for 2015–2018 from the University of Montana Analysis (Millspaugh and Clawson 2019) are provided for context.

DISCUSSION

In this report, we provide results from an updated analysis of elk age-at-harvest data using SPR models to estimate elk population sizes in Kentucky during 2019–2022. Our total population estimates provide increased confidence that the elk population in Kentucky has hovered around 10,000 individuals since 2018, possibly reaching a maximum of approximately 11,000 individuals during 2021–2022. Much of this population increase appears to have been due to an increasing female component of the population, possibly facilitated by lower female harvest rates. In contrast, low survival rates among all male age classes, particularly adult males, has likely led to stabilization of the male component of the population since 2018. The lower male survival rates that we documented were not caused solely by legal harvest but were instead the result of compounding effects between moderate non-harvest mortality that was followed by moderate to high harvest mortality. Given much of the non-harvest mortality documented in males was from unknown/unidentified causes, direct management actions to mitigate this mortality are difficult to identify or prescribe.

Nevertheless, our estimates indicate that the elk population in Kentucky is likely still experiencing long-term positive population growth, despite possible declines during some years. Such undulations in population size among years should be expected and exemplify why a single estimate for one year provides a ‘snapshot’ that may not be indicative of true ungulate population trends. Compared to other abundance-estimation methods, SPR models may not provide the most accurate or precise population size estimates within a single year, particularly for the most recent years of a timeseries (Fieberg et al. 2010); however, SPR models can provide accurate population trend estimates, even with few years of age-at-harvest data, if sufficient auxiliary data

are available (Fieberg et al. 2010, Clawson et al. 2013). Long-term population trend monitoring is often the most useful for management of secure but harvested ungulate populations (Krausman and Cain 2013). Additionally, as more years of age-at-harvest data are collected and added to the timeseries, along with continued monitoring of hunter effort and auxiliary information, SPR-estimated abundances should have improved accuracy and precision (Skalski et al. 2012, Clawson et al. 2013).

Although previous researchers derived similar population size ($N = 10,000$) and growth rate ($\lambda = 1.13$) estimates for elk in Kentucky during 2013–2014 (Popp et al. 2014), those derivations were based on expert opinion responses to survey questionnaires, not empirical data, and consequently had unknown reliability. Indeed, those derived estimates were substantially larger than the empirical estimates for the same year produced by the proof-of-concept University of Montana Analysis that used SPR models (Millsbaugh and Clawson 2019). This indicated that the derivations in Popp et al. (2014) were overly optimistic, as is often the case when basing estimations on expert opinion rather than empirical data, largely due to cognitive biases (Colson and Cooke 2018, Moore et al. 2022). In contrast, a 2006–2007 population estimate of 7,000 elk (95% CI = 5,488–8,514) based on aerial forward-looking infrared radiography (FLIR) surveys and a landscape-based model may have been reasonably accurate (Dahl 2008). Our estimates for 2019–2022, which build on the University of Montana Analysis, were based on empirical age-at-harvest, survival, mortality, and hunter effort data that were collected specifically within an SPR framework and therefore should be considered more reliable.

Multiple improvements in data collection occurred since the proof-of-concept SPR analysis was conducted by University of Montana, which undoubtedly improved abundance estimate reliability. For instance, the implementation of a mandatory post-season hunter survey with focused effort questions (e.g., ‘how many days did you spend scouting’ and ‘how many days did you spend hunting’) allowed us to calculate and use a much better hunter effort metric than was available for the University of Montana Analysis (i.e., number of permits purchased). Not only did this Commission-recommended, legislature-approved survey provide an improved hunter effort metric, but it also facilitated the ability to estimate permit type (method)-specific hunter effort and elucidate similarities and differences in hunter effort among those permit types. Additionally, the massive geographical expansion of elk radio-collaring efforts throughout the Elk Restoration Zone that occurred during 2019–2022 for both sexes provided a wealth of representative, population-level auxiliary data for integration into the SPR models. In contrast, most of the radio-collar monitoring data that were available for use in the University of Montana Analysis were obtained from hypothesis-driven research studies conducted on Limited Entry Areas, where harvest rates were abnormally high and likely not representative of the broader Elk Restoration Zone (Slabach et al. 2018). Furthermore, no calf survival data were available for use in the University of Montana Analysis, whereas a new calf survival study was initiated during 2020 that provided three consecutive years of intensive monitoring data across the Elk Restoration Zone for estimating auxiliary calf survival and mortality probabilities at the population-level.

We caution that our elk population size estimates for 2019–2022 may be biased for two primary reasons. First, small sample sizes in the age-at-harvest data for each permit (method) type, particularly for females, prevented us from estimating method-specific abundances. Although we could estimate firearm- and archery-specific abundances for male elk, models for the other permit types (e.g., youth, landowner, Commission, etc.) did not converge for males, and

low harvest rates for females prevented method-specific model fitting altogether. Thus, we were forced to pool the age-at-harvest data among permit types for each sex to achieve model convergence, which necessarily ignored much of the heterogeneity inherent to the age-at-harvest data and hunter effort for each permit type. The only approach for overcoming said issue would be to increase the number of annual permits, particularly for the other permit types (youth, landowner, Commission, etc.) and for females in general; however, based on the SPR models' most recent abundance estimates and elk population biology, we do not advise increasing permits at this time, assuming KDFWR's objective is to maintain a stable to increasing elk population. Second, although the proportion of harvested males that were aged via tooth extraction and cementum annuli analysis has remained relatively constant (40–48% per year), the number of harvested females that were aged via cementum annuli analysis declined substantially to a low of just 13%. Consequently, most age classes specified for harvested females were based on visual examinations, which can be fraught with inaccuracies even if conducted by trained experts, such as agency biologists (Williams et al. 2011, Gee et al. 2014, Beausoleil and Warheit 2015). Because of the low tooth-aging proportion, we were forced to assume that most of the field-ages based on visual examinations were accurate for females, which may have biased our female abundance estimates to an unknown but potentially high magnitude (Murphy et al. 2022). Therefore, it is imperative that actions are taken to attempt to increase elk hunter participation in the tooth mail-in program.

CONCLUSIONS AND RECOMMENDATIONS

By expanding on the seminal SPR modeling conducted in the University of Montana Analysis, our SPR analysis provides additional justification for using SPR models to estimate abundance and monitor population trends of elk in Kentucky. Additionally, combined with the results of the University of Montana Analysis, our collective findings very strongly support long-term reintroduction success of elk in Kentucky, despite enduring genetic isolation (Muller et al. 2018, Youngmann et al. 2020). Similar to the Big South Fork black bear (*Ursus americanus*) population, these results provide additional evidence that rapid, sustained population growth post-reintroduction can effectively mitigate the development of deleterious genetic and demographic effects in isolated large mammal populations (Murphy et al. 2015, 2019a).

We note that our analyses were based primarily on data collected during 2019–2022 to provide a comparison with the proof-of-concept conducted by University of Montana, in which auxiliary and hunter effort data were not collected in an SPR framework. By implementing most of the recommendations in the University of Montana Analysis, KDFWR and UK collaboratively obtained better hunter effort data and more representative survival and mortality data, all of which facilitated surprisingly precise elk abundance estimates with relatively few years of age-at-harvest data. Our next step is to include the 2014–2017 age-at-harvest data with the 2018–2022 data to attempt to produce abundance estimates over a longer time series, which theoretically should improve estimate precision and reliability. However, given the non-negligible changes to harvest structure (e.g., permit types and seasons) that occurred between 2014 and 2022, integration of age-at-harvest data from earlier years with more recent years may not be possible. Nevertheless, maintaining a harvest structure for the 2023–2024 season that is similar to what occurred during 2019–2022 will provide a fifth year of data for inclusion in a subsequent SPR analysis, which likely will also improve estimate precision.

Although many of the recommendations from the University of Montana Analysis were implemented, some were not and, therefore, we reiterate those here because some deficiencies remain that may have led to bias in abundance estimates:

1. The severe decline in harvested female elk tooth submissions by hunters for aging via cementum annuli analysis that has occurred over the last 4 years is a major hindrance. A foundational assumption of SPR models is that the ages of harvested individuals are accurately determined, and cementum annuli analysis of extracted teeth is generally considered the most reliable method for elk. Basing ages on visual examinations is problematic, often inaccurate, and can result in biased abundance estimates from SPR models. Therefore, we reiterate the previous recommendations from the Elk Program Staff and the University of Montana Analysis that actions must be taken to increase hunter participation in the tooth mail-in program. The currently unenforced, voluntary tooth submission program has a rapidly dwindling participation rate among elk hunters in Kentucky, which is having a direct negative impact on the quality and precision of female and total elk population abundance estimates from SPR models.
2. Despite substantial improvements in auxiliary data collection, one drawback remains, which is survival and mortality probabilities of yearling males. Across the 4 years of radio-collar monitoring, survival and mortality data were obtained for just 15 total male yearlings. This small sample size of auxiliary data led to incongruous mortality probabilities between the CIFs estimated from radio-collar data and the probabilities estimated by SPR models for this age class. Although understandably difficult to accomplish in practice, attempting to increase the sample size of radio-collared male yearlings would provide more representative auxiliary data for integration in the SPR models, which should further improve both male and total population abundance estimates.
3. Although SPR models can produce reliable estimates of population trends, the point estimates of abundance within a given year are often biased or imprecise, particularly for the most recent years of a time series. Obtaining an independent estimate of abundance at infrequent intervals using other methods, such as spatial capture-recapture or mark-resight approaches, which is then integrated in the SPR models as auxiliary data, can help calibrate and minimize bias in SPR-estimated abundances. Therefore, we recommend beginning discussions for development of a population-wide capture-recapture or mark-resight survey in the spatially explicit framework that could be implemented at 5–10-year intervals to calibrate the SPR model abundance estimates. Currently, spatially clustered sampling designs provide the most effective and efficient approach for obtaining data across large geographical areas and estimating population size and density within a single year. Given the number and distribution of radio-collared elk already on the landscape, simply deploying clusters of camera-traps across the Elk Restoration Zone in a spatial mark-resight framework would likely provide the necessary data to estimate abundance in one year. This spatially explicit clustered camera-trapping approach was recently applied to an area the size of the Elk Restoration Zone to efficiently estimate population size and density of another large mammal with high precision (Murphy et al. 2019b).

ACKNOWLEDGMENTS

We thank KDFWR for funding for this study and Elk Program Staff for assisting with field work, data collection, and data compilation. In particular, we are grateful for the contributions from John Hast, Joe McDermott, Dan Crank, and Mark Peterson. We also thank the multiple KDFWR biologists, technicians, and law enforcement officers, and the UK technicians, students, and volunteers, who assisted with the field work for data collection. Finally, we thank Kentucky elk hunters for answering the effort-related questions on the post-hunt surveys, providing tooth samples for aging, and supporting this project.

REFERENCES

- Beausoleil, R.A., and Warheit, K.I. 2015. Using DNA to evaluate field identification of cougar sex by agency staff and hunters using trained dogs. *Wildlife Society Bulletin* 39:203-209.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378-400.
- Clawson, M.V. 2015. *Management application of statistical population reconstruction to wild game populations*. Dissertation, University of Washington, Seattle, USA.
- Clawson, M.V., Skalksi, J.R., Lady, J.M., Hagen, C.A., Millspaugh, J.J., Budeau, D., and Severson, J.P. 2017. Performing statistical population reconstruction using program PopRecon 2.0. *Wildlife Society Bulletin* 41:581-589.
- Clawson, M.V., Skalski, J.R., and Millspaugh, J.J. 2013. The utility of auxiliary data in statistical population reconstruction. *Wildlife Biology* 19:147-155.
- Colson, A.R., and Cooke, R. 2018. Expert elicitation: Using the Classical Model to validate experts' judgements. *Review of Environmental Economics and Policy* 12:113-132.
- Cox, J.J. 2011. Tales of a repatriated megaherbivore: Challenges and opportunities in the management of reintroduced elk in Appalachia. Pages 632-643 in Fei, S., Lhotka, J.M., Stringer, J.W., Gottschalk, K.W., and Miller, G.W. (eds.). *Proceedings of the 17th central hardwood forest conference*. U.S. Department of Agriculture Forest Service, Newtown Square, USA.
- Davis, M.L., Berkson, J., Steffen, D., and Tilton, M.K. 2007. Evaluation of accuracy and precision of Downing population reconstruction. *Journal of Wildlife Management* 71:2297-2303.
- Dhal, L.M. 2008. *Using forward-looking infrared radiography to estimate elk density and distribution in eastern Kentucky*. Thesis, University of Kentucky, Lexington, USA.
- Downing, R.L. 1980. Vital statistics of animal populations. Pages 247-267 in Schemnitz, S.D. (ed.). *Wildlife techniques manual*. The Wildlife Society, Washington D.C., USA.
- Erb, J.D., and Boyce, M.S. 1999. Distribution of population declines in large mammals. *Conservation Biology* 13:199-201.
- Fieberg, J.R., Shertzer, K.W., Conn, P.B., Noyce, K.V., and Garshelis, D.L. 2010. Integrated population modeling of black bears in Minnesota: Implications for monitoring and management. *PLoS ONE* 5:e12114.

- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., and Sibert, J. 2012. AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27:233-249.
- Fry, F.E. 1949. Statistics of a lake trout fishery. *Biometrics* 5:26-67.
- Gast, C., Skalski, J.R., and Beyer, D.E. 2013. Evaluation of fixed- and random-effects models and multistage estimation procedures in statistical population reconstruction. *Journal of Wildlife Management* 77:1258-1270.
- Gee, K.L., Webb, S.L., and Holman, J.H. 2014. Accuracy and implications of visually estimating age of male white-tailed deer using physical characteristics from photographs. *Wildlife Society Bulletin* 38:96-102.
- Gotelli, N.J. 2008. *A primer of ecology*. Sinauer Associates, Sunderland, USA.
- Gove, N.E., Skalski, J.R., Zager, P., and Townsend, R.L. 2002. Statistical models for population reconstruction using age-at-harvest data. *Journal of Wildlife Management* 66:310-320.
- Gray, B. 2022. cmprsk: Subdistribution analysis of competing risks. R package version 2.2-11. <https://cran.r-project.org/package=cmprsk>.
- Gulland, J.A. 1965. Estimation of mortality rates. *Annex to Arctic Fisheries Working Group Report, document #3*. International Council for the Exploration of Sea, Copenhagen, Denmark.
- Hast, J.T. 2019. *Vital rates and habitat selection of bull elk (Cervus canadensis nelsoni) in southeast Kentucky*. Dissertation, University of Kentucky, Lexington, USA.
- Hatter, I.W., Mowat, G., and McLellan, B.N. 2018. Statistical population reconstruction to evaluate grizzly bear trends in British Columbia, Canada. *Ursus* 29:1-12.
- Heisey, D.M., and Patterson, B.R. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544-1555.
- Howard, A.L., Clement, M.J., Peck, F.R., and Rubin, E.S. 2020. Estimating mountain lion abundance in Arizona using statistical population reconstruction. *Journal of Wildlife Management* 84:85-95.
- Johnson, R.D., Jenks, J.A., Tucker, S.A., and Wilckens, D.T. 2019. Mountain lion (*Puma concolor*) population characteristics in the Little Missouri Badlands of North Dakota. *American Midland Naturalist* 181:207-224.
- Kanarek, A.R., Webb, C.T., Barfield, M., and Holt, R.D. 2015. Overcoming Allee effects through evolutionary, genetic, and demographic rescue. *Journal of Biological Dynamics* 9:15-33.
- Kentucky Department of Fish and Wildlife Resources (KDFWR). 2016. *2015–2030 Kentucky elk management plan*. KDFWR, Frankfort, USA.
- Krausman, P.R., and Cain, J.W. 2013. *Wildlife management and conservation: Contemporary principles and practices*. Johns Hopkins University Press, Baltimore, USA.
- Larkin, J.L., Grimes, R., Cornicelli, L., Cox, J.J., and Maehr, D.S. 2001. Returning elk to Kentucky: Foiling Murphy's Law. Pages 101-117 in Maehr, D.S., Noss, R.F., and Larkin, J.L. (eds.). *Large mammal restoration: Ecological and sociological challenges in the 21st century*. Island Press, Washington D.C., USA.
- Larkin, J.L., Maehr, D.S., Cox, J.J., Bolin, D.C., and Wichrowski, M.W. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. *Journal of Wildlife Management* 67:467-476.

- Lenth, R.V. 2023. emmeans: Estimated marginal means, aka least-squares means. R package version 1.8.6. <https://cran.r-project.org/package=emmeans>.
- Louw, C.J., Ferreira, S.M., and Marshal, J.P. 2022. Water dependence structures predation risk for large herbivores in insular protected areas. *Mammalian Biology* 102:1783-1792.
- Lüdtke, D. 2018. ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software* 3:772.
- Millsbaugh, J.J., and M.V. Clawson. 2019. *Kentucky elk statistical population reconstruction modeling project update*. Final Report to Kentucky Department of Fish and Wildlife Resources, University of Montana, Missoula, USA.
- Moore, J.F., Martin, J., Waddle, H., Campbell Grant, E.H., Fleming, J., Bohnett, E., Akre, T.S.B., Brown, D.J., Jones, M.T., Meck, J.R., Oxenrider, K., Tur, A., Willey, L.L., and Johnson, F. 2022. Evaluating the effect of expert elicitation techniques on population status assessment in the face of large uncertainty. *Journal of Environmental Management* 306:114453.
- Muller, L.I., Murrow, J.L., Lupardus, J.L., Clark, J.D., Yarkovich, J.G., Stiver, W.H., Delozier, E.K., Slabach, B.L., Cox, J.J., and Miller, B.F. 2018. Genetic structure in elk persists after translocation. *Journal of Wildlife Management* 82:1124-1134.
- Murphy, S.M., Cox, J.J., Augustine, B.C., Hast, J.T., Guthrie, J.M., Wright, J., McDermott, J., Maehr, S.C., and Plaxico, J.H. 2016. Characterizing recolonization by a reintroduced bear population using genetic spatial capture-recapture. *Journal of Wildlife Management* 80:1390-1407.
- Murphy, S.M., Cox, J.J., Clark, J.D., Augustine, B.C., Hast, J.T., Gibbs, D., Strunk, M., and Dobey, S. 2015. Rapid growth and genetic diversity retention in an isolated reintroduced black bear population in the central Appalachians. *Journal of Wildlife Management* 79:807-818.
- Murphy, S.M., Eriksen-Meier, S., Robertson, L., and Elbroch, L.M. 2022. Is unreliable science guiding bobcat management in Wyoming and other western U.S. states? *Ecological Solutions and Evidence* 3:e12116.
- Murphy, S.M., Hast, J.T., Augustine, B.C., Weisrock, D.W., Clark, J.D., Kocka, D.M., Ryan, C.W., Sajecki, J.L., and Cox, J.J. 2019a. Early genetic outcomes of American black bear reintroductions in the central Appalachians, USA. *Ursus* 29:119-133.
- Murphy, S.M., Wilckens, D.T., Augustine, B.C., Peyton, M.A., and Harper, G.C. 2019b. Improving estimation of puma (*Puma concolor*) population density: Clustered camera-trapping, telemetry data, and generalized spatial mark-resight models. *Scientific Reports* 9:4590.
- Murray, D.L., and Patterson, B.R. 2006. Wildlife survival estimation: Recent advances and future directions. *Journal of Wildlife Management* 70:1499-1503.
- Ng, V.K.Y., and Cribbie, R.A. 2017. Using the gamma generalized linear model for modeling continuous, skewed and heteroscedastic outcomes in psychology. *Current Psychology* 36:225-235.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. 1989. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 53:7-15.
- Popp, J.N., Toman, T., Mallory, F.F., and Hamr, J. 2014. A century of elk restoration in eastern North America. *Restoration Ecology* 22:723-730.
- R Core Team. 2023. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Robert, A., Colas, B., Guigon, I., Kerbiriou, C., Mihoub, J.B., Saint-Jalme, M., and Sarrazin, F. 2015. Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. *Animal Conservation* 18:397-406.
- Roseberry, J.L., and Woolf, A. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. *Wildlife Monographs* 117:3-59.
- Skalski, J.R., Clawson, M.V., and Millspaugh, J.J. 2012. Model evaluation in statistical population reconstruction. *Wildlife Biology* 18:225-234.
- Skalski, J.R., Townsend, R.L., and Gilbert, B.A. 2007. Calibrating statistical population reconstruction models using catch-effort and index data. *Journal of Wildlife Management* 71:1309-1316.
- Slabach, B.L., Hast, J.T., Murphy, S.M., Bowling, W.E., Crank, R.D., Jenkins, G., Johannsen, K.L., and Cox, J.J. 2018. Survival and cause-specific mortality of elk *Cervus canadensis* in Kentucky, USA. *Wildlife Biology* 2018:1-9.
- Southern, D.A., Faris, P.D., Brant, R., Galbraith, P.D., Norris, C.M., Knudtson, M.L., Ghali, W.A., and for the APPROACH Investigators. 2006. Kaplan- Meier methods yielded misleading results in competing risk scenarios. *Journal of Clinical Epidemiology* 59:1110-1114.
- Szücs, M., Melbourne, B.A., Tuff, T., Weiss-Lehman, C., and Hufbauer, R.A. 2017. Genetic and demographic founder effects have long-term fitness consequences for colonising populations. *Ecology Letters* 20:436-444.
- Therneau, T.M. 2023. survival: A package for survival analysis in R. R package version 3.5-5. <https://cran.r-project.org/package=survival>.
- Therneau, T.M., and Grambsch, P.M. 2000. *Modeling survival data: Extending the Cox model*. Springer, New York, USA.
- Williams, B.W., Etter, D.R., Dewitt, P.D., Scribner, K.T., and Friedrich, P.D. 2011. Uncertainty in determination of sex from harvested bobcats. *Journal of Wildlife Management* 75:1508-1512.
- Wolkewitz, M., Cooper, B.S., Bonten, M.J.M., Barnett, A.G., and Schumacher, M. 2014. Interpreting and comparing risks in the presence of competing events. *BMJ* 349:g5060.
- Youngmann, J.L., Deyoung, R.W., Demarais, S., Strickland, B.K., and Jenkins, G. 2020. Genetic characteristics of restored elk populations in Kentucky. *Journal of Wildlife Management* 84:515-523.