

Estimating Elk Abundance Using the Lincoln-Petersen Method

Braiden A. Quinlan¹, Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, 310 West Campus Drive, Blacksburg, VA 24061

Jacalyn P. Rosenberger, Virginia Department of Wildlife Resources, 1796 Highway 16, Marion, VA 24354

David M. Kalb, Rhode Island Department of Environmental Management, 235 Promenade Street, Providence, RI 02908

Emily D. Thorne, Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, 310 West Campus Drive, Blacksburg, VA 24061

W. Mark Ford, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, 310 West Campus Drive, Blacksburg, VA 24061

Michael J. Cherry, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Blvd, MSC 218, Kingsville, TX 78363

Abstract: Achieving a target population size is often the first goal of species restorations. From 2012 to 2014, the Virginia Department of Wildlife Resources released 75 elk (*Cervus canadensis*) originating from Kentucky into Buchanan County in southwestern Virginia. These individuals were ear tagged with unique numbers upon release with an additional 33 elk tagged within the Virginia Elk Management Zone (VEMZ) from 2019 through early 2022. To assess post-release population size, we conducted visual driving surveys throughout Buchanan County from January through mid-April, 2021 and January through March, 2022, counting elk and noting sex, age class, and tagged individuals when observed. We conducted four surveys annually, each consisting of pooled elk counts from eight driving routes, and calculated a Lincoln-Petersen population estimate with Chapman's bias correction for each survey, then averaged estimates for each year. The population estimate in Buchanan County was 250 (95% CI: 100–400) elk in 2021 and 303 (155–452) in 2022. Our elk population estimates indicate Virginia is on the trajectory of meeting the first goal in their 2019–2028 elk management plan of achieving a viable elk population.

Key words: *Cervus canadensis*, population size, southwest Virginia, species restoration

Journal of the Southeastern Association of Fish and Wildlife Agencies 10:135–141

Human activity has altered landscapes and led to worldwide extinctions and local extirpations for many species (Vitousek et al. 1997). Restoring species to portions of their former distribution is a tool that managers can use to help reduce or reverse extirpations and reestablish ecosystem integrity and function. The restored species may initially have access to abundant resources and face low intraspecific competition (Larter et al. 2000, Larkin et al. 2003, Stadtmann and Seddon 2020). As wildlife in North America is a public resource, stakeholders benefit from increased recreational opportunities, such as hunting and viewing, but also through provided ecosystem services (Chapagain and Poudyal 2020, Brazier et al. 2021). However, landscapes at the time of restoration efforts may have changed vastly during the time since extirpation, and often it is unknown whether the reintroduced species can successfully adapt and produce locally to regionally viable populations (Carroll et al. 2003, James and Eldridge 2007).

Elk (*Cervus canadensis*) were once distributed across the eastern

United States (U.S.) ranging from the Midwest to the Eastern Seaboard (Murie 1951). Following European settlement, elk numbers declined from overharvest and habitat loss that resulted in extirpation east of the Mississippi River before the end of the 19th century (VDWR 2019, Lituma et al. 2021). In the state of Virginia, the last elk was harvested in 1855 (Murie 1951). This extirpation coincided with the beginning of the commercial coal industry and large-scale logging in southwest Virginia (Hibbard 1990). At the turn of the 20th century, reintroduction of elk from populations in the western U.S. and private Virginian stock was attempted into the Ridge and Valley portion of southwest Virginia. However, due to forest maturation, poaching, and conflict with agriculture, elk were once again extirpated by 1970 (VDWR 2019). Conversely, in the 1990s following large-scale surface mining for coal, abundant open areas existed in the Appalachian Plateau region (hereinafter, Coalfields), prompting the state of Kentucky to undertake what ultimately became a highly successful elk reintroduction program (Popp et al.

1. E-mail: braidenq@vt.edu

2014). Building on this success and to supplement herds being established via immigration from reintroductions in Kentucky and later in Tennessee, Virginia and West Virginia implemented their own elk reintroductions in the Coalfields (VDWR 2019). Accordingly, development and assessment of viable population estimation approaches would be beneficial to evaluate elk reintroductions in the Coalfields.

The Lincoln-Petersen method is one such approach that employs simple techniques in both data collection and analysis. Managers have used the Lincoln-Petersen method, or variations thereof, for estimating animal abundances for decades (Petersen 1896, Lincoln 1930), including for ungulates (Bartmann et al. 1987, Lopez et al. 2004, Curtis et al. 2009, McIntosh et al. 2009, Boulanger et al. 2018). Therefore, we sought to estimate the current elk population in Buchanan County in southwest Virginia during 2021 and 2022 using the Lincoln-Petersen method with a mark-resight data collection approach. We expected Lincoln-Petersen indices to provide viable yearly population estimates, and based on anecdotal observations, we expected the elk population to increase between our 2021 and 2022 survey efforts.

Study Area

The Virginia Elk Management Zone (VEMZ) comprises Buchanan, Dickenson, and Wise counties in southwest Virginia bordering southern West Virginia and eastern Kentucky. The VEMZ is located in the central Appalachian Mountains, part of the Appalachian Plateau physiographic sub-province (Powell 1895). Second- and third-growth Appalachian oak (*Quercus* spp.) dominate this area with diverse cove and mixed mesophytic hardwood forest types that included American beech (*Fagus grandifolia*), basswood (*Tilia americana*), black cherry (*Prunus serotina*), eastern hemlock (*Tsuga canadensis*), maples (*Acer* spp.), pignut hickory (*Carya glabra*), white ash (*Fraxinus americana*), and yellow-poplar (*Liriodendron tulipifera*; Braun 1942, Clark 2012). However, second to forest cover in extent, the region has a long history of coal mining, with surface mining increasing in land cover area (7.1% of land) since the 1970s (Pericak et al. 2018). In this portion of the Coalfields, surface mine size ranges from <60 ha to >5000 ha of contiguous land. Within the VEMZ, we focused on Buchanan County, specifically near the original Virginia elk release site. Thirty-year average monthly precipitation for this area ranged from 6.6 cm in November to 14.5 cm in July, with greatest snowfall during January, averaging 15.7 cm per year (NOAA 2022). Average monthly temperatures during the same period ranged from 0.9 C in January to 22.7 C in July (NOAA 2022). Elevations are

238–1,129 m above sea level and the topography is characterized by rugged, precipitous slopes with narrow incised valleys.

Methods

Elk were fitted with GPS radio collars (G5-2D, Advanced Telemetry Systems, Isanti, Minnesota, USA¹) and ear tagged (7.62 cm cattle tags) with a unique number upon release to the VEMZ, or subsequently thereafter from opportunistic captures by the Virginia Department of Wildlife Resources. To enumerate elk, we drove eight routes distributed within a 95% minimum convex polygon of all elk locations from 2012–2020. Our routes spanned multiple landcover types (two on mines and reclaimed mines, two in wooded areas, two around managed pastureland, and two along paved roads in more developed areas). We drove each route four times each year, during January through mid-April 2021 and January through late March 2022. To avoid bias from driving direction, we drove the four routes (1) forwards in the morning, (2) forwards in the evening, (3) backwards in the morning, and (4) backwards in the evening (Lopez et al. 2004). Morning routes began at sunrise and evening routes ended at sunset. When driving the routes, we maintained a speed of 16 km h⁻¹ on unimproved roads and ≤40 km h⁻¹ on paved roads. A driver and an additional observer were inside the vehicle for each route (Lopez et al. 2004, Roberts et al. 2006). When we observed elk, the driver moved to the side of the road if necessary and both observers began counting the number of individuals in the group using binoculars (Lopez et al. 2004). We recorded the number of elk in the group, number of bulls, cows, and calves, number of tagged individuals, and when possible, identified all unique individuals based on their ear tag number (Lopez et al. 2004, Roberts et al. 2006). Elk were not counted on back-tracked portions of routes to avoid double-counts (Roberts et al. 2006).

We pooled elk observations across the eight routes by sampling period within each year, for a combined four sampling periods each year (hereinafter, surveys). To limit violation of Lincoln-Petersen method assumptions regarding population closure and absence of tag loss (Otis et al. 1978), we only considered elk tagged from 2019 onward as available for observation in our study. To establish the likely proportion of tagged but unidentifiable elk, we calculated the ratio of all confirmed elk tagged from 2019 until the first survey of the year to all identifiable tags observed during all surveys from that year. We used that ratio to adjust the tagged but unidentifiable elk observed during our surveys. For example, of the tagged elk we uniquely identified during the surveys in a year, if 50% had been tagged since 2019, we assumed 50% of the elk we could not identify during a given survey were likely tagged since 2019.

1. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

We calculated Lincoln-Petersen population estimates with Chapman's bias correction (Chapman 1951) in R (R Core Team 2020, Rivest et al. 2022) for each survey. For each year we calculated the mean of the four survey estimates (Bartmann et al. 1987) and 95% confidence intervals around each mean using the *t* statistic and estimated standard error of each yearly mean. We rounded all population estimates down to the nearest whole elk (Otis et al. 1978).

Results

Between 2012 and the start of surveys in 2022, 108 elk were tagged by Virginia Department of Wildlife Resources. Of the 75 elk tagged upon release into the VEMZ from 2012 to 2014, 66 were thought to be alive at the start of the 2022 surveys (2012: *n* = 15; 2013: *n* = 9; 2014: *n* = 42). Of the 33 elk tagged between 2019 and the start of surveys in 2022 (2019: *n* = 20; 2020: *n* = 9; 2021: *n* = 3; 2022: *n* = 1), three died prior to the start of 2021 surveys and three others were tagged outside of the survey area. Additionally, seven previously tagged elk were re-tagged in 2019–2020. As a result, 26 and 27 elk from our specified capture window were assumed available for observation during 2021 and 2022 surveys, respectively. Our four surveys covered a total of 836 km each year. During both 2021 and 2022, we observed elk on routes 1, 3, and 6 (Figure 1). We observed elk on routes 1 and 3 during every survey period, whereas we observed elk on route 6 during one survey each year.

Of the 26 and 27 tagged elk we considered available for observation during the 2021 and 2022 survey periods, respectively, we did not confirm the observation of 12 of these individuals during the 2021 surveys, and eight of these individuals during the 2022 surveys. Six individuals were not uniquely identified during either 2021 or 2022 surveys, three of which were the only male elk tagged during our study. However, one individual observed during 2021 was not observed during 2022, whereas six individuals not seen during 2021 surveys were observed during the 2022 surveys.

Upon completing the surveys, the proportions of confirmed tags since 2019 relative to confirmed tags total was 0.563 (27/48) and 0.564 (44/78) during 2021 and 2022, respectively. We therefore included four of seven unknown tagged elk for both 2021 and 2022 surveys rounding our proportion up to the nearest whole integer. This provided slightly more conservative population estimates for each year (Table 1). Average population estimates were 250 (SE = 94.3; 95% CI = 100–400) and 303 (93.32; 155–452) elk for 2021 and 2022, respectively. During 2021, we calculated calf and sex ratios of 42 calves and 89 bulls per 100 cows. During 2022, the ratios changed slightly to 38 calves and 66 bulls per 100 cows.

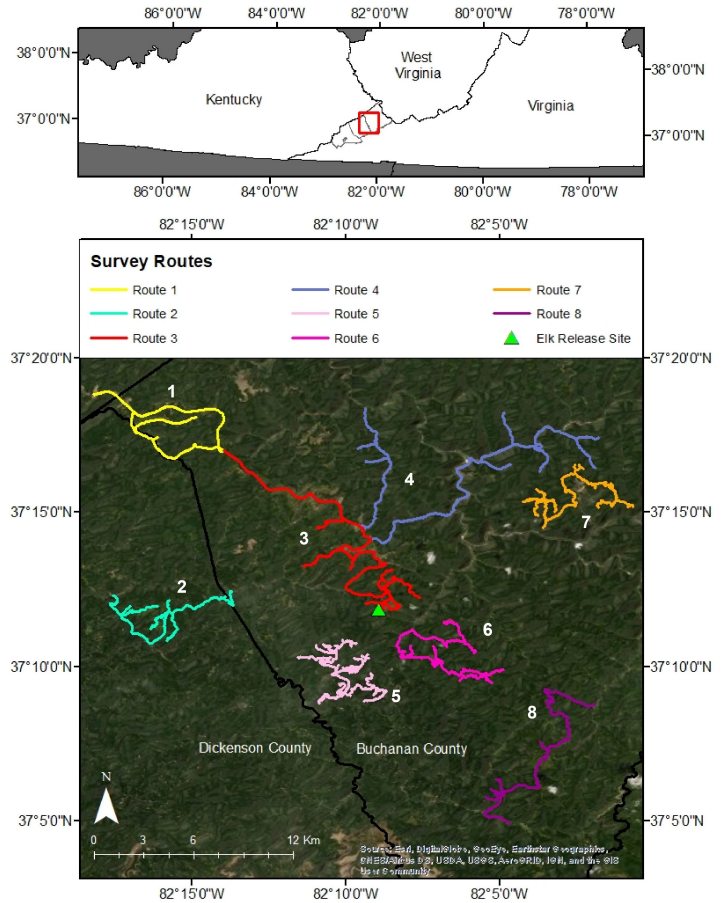


Figure 1. Eight elk survey routes within the Virginia Elk Management Zone (VEMZ; outlined gray counties in southwestern Virginia), specifically around the elk release site in Buchanan County, Virginia (green triangle), surveyed from January through mid-April 2021 and January through March 2022. We observed elk on routes 1, 3, and 6 both years with no elk observed on any other route either year.

Table 1. Survey counts and population estimates (from Lincoln-Petersen mark-recapture estimator with Chapman's bias correction) for elk in Buchanan County, southwest Virginia, during 2021 and 2022.

Year	Survey	Total tagged	Observed elk	Observed tagged	Estimate (SE)
2021	1	26	119	15	201 (29)
	2		56	3	383 (153)
	3		56	8	170 (41)
	4		54	5	246 (78)
2022	1	27	107	6	431 (128)
	2		121	11	283 (57)
	3		168	15	294 (45)
	4		125	16	206 (29)

Discussion

An important measure of the progress and success of an animal restoration is population size. In the case of elk in southwestern Virginia, these data can help inform hunting program implementation, habitat management, and human-wildlife conflict resolution. Repeated Lincoln-Petersen surveys can provide sound

population estimates without requiring logistically difficult field surveys or complicated and data-intensive analyses. As expected, our 2022 point estimate of population size was greater than our 2021 estimate. More importantly, since the completion of the elk restoration in 2014, the elk population in Virginia has increased approximately four-fold compared to what was released in the area (VDWR 2019).

Sex and cow:calf ratios are important indicators of herd health and the potential for population growth (Larkin et al. 2003, Keller et al. 2015). For elk, the fastest population growth rates occur when approximately 75% of the population are female (Keller et al. 2015). Although we observed much lower cow:bull ratios (100:89 and 100:66 for 2021 and 2022, respectively) than those associated with the fastest modeled growth rates observed by Keller et al. (2015; 100:25), we posit that this simply indicates a slower rate of increase rather than stability or decline. Additionally, across elk populations in the eastern and midwestern United States where reintroduction has occurred, the average number of juveniles per adult female is 0.80 for established populations (Keller et al. 2015) but ranges from 0.51 in North Carolina (Murrow et al. 2009) to 0.96 in Kansas (Conrad 2009). We observed considerably fewer juveniles per female for an established population at 0.42 and 0.38 juveniles per cow in 2021 and 2022, respectively. Our estimates might be conservative, however, as we did not separate adult and subadult females during our surveys due to difficulty differentiating them at a distance.

Although we conducted surveys across several months, based on our GPS locations and individuals observed within groups during routes, prior research on habitat quality, and minimal energy requirements and movement during winter (Craighead et al. 1973, Harestad and Bunnell 1979), we reasonably assumed the population was closed within the yearly survey periods. Additionally, we are confident there were no double-counts of elk within surveys for these same reasons. Our GPS and survival data for almost half of the tagged individuals each year (2021: 12; 2022: 11) showed no mortality nor movement outside of the survey area for those individuals. However, we had six tagged elk that were never observed during either survey year. With public tours, other viewing opportunities, heavily used recreational trails, and intensive monitoring by area land managers, we think it is unlikely a tagged individual would die without our knowledge, nonetheless mortality is a possibility. However, prior to the start of surveys in 2021, or between 2021 and 2022 survey periods, elk in our study area could have immigrated to or emigrated from Kentucky due to the proximity to other herds there. Prior to the restoration of elk in Virginia and the establishment of the VEMZ, elk had been crossing into Virginia from Kentucky since 1998 and some individuals were

harvested in Buchanan and Wise Counties prior to the elk hunting prohibition in the VEMZ in 2011 (Larkin et al. 2001, VDWR 2019). Three of the six tagged elk we never observed were the only three bulls tagged during our study. These bulls may have left the survey area as bull elk disperse at higher rates than cows (Edge et al. 1986), potentially making them unavailable for observation during our survey periods.

To meet the Lincoln-Petersen method assumption that individuals retain their marks, we only included elk tagged between 2019 and the beginning of the survey period. We assumed all tagged elk retained at least one ear tag throughout the study consistent with other studies (Beasom and Burd 1983, Alt et al. 1985, Seroussi et al. 2011). For example, Beasom and Burd (1983) found 100% tag retention in white-tailed deer (*Odocoileus virginianus*) after one year and 95% tag retention in mule deer (*Odocoileus hemionus*) after two years where two individuals lost a single tag during that time. However, our assumption about tag retention is non-trivial, as different assumptions about tag loss would have decreased our assumed number of tagged individuals available for observation and therefore decreased the resulting population estimates.

An additional assumption of the Lincoln-Petersen method is that all marks are accurately recorded at each observation occasion (Otis et al. 1978). We accurately recorded all unique individuals when possible. For both years, we could not identify seven marked individuals due to angle of observation, dirty tags, or distance. We created a ratio of confirmed individuals tagged since 2019 to the total number of confirmed tagged individuals regardless of when they were tagged to make use of observations of unknown individuals because excluding them would skew the population estimate. We used this ratio to include four of the seven unknown elk as tagged between 2019 and the start of the survey year. While we cannot rule out the possibility that more of the seven unidentified individuals were tagged prior to or after 2019, we viewed our adjustment as making reasonable use of the available data.

The Lincoln-Petersen method also assumes that each individual has an equal probability of capture on each trapping occasion, and that marks do not affect the resight or recapture of the animal (Otis et al. 1978). Adult female elk were the target for tags from 2019 through our last survey period because they are demographically important individuals to monitor when assessing population growth (Gaillard et al. 1998, Evans et al. 2006). The three bulls included in our study were opportunistically captured and tagged. Between 2019 and the start of the 2021 survey period, we considered 26 tagged elk available for observation with an additional elk tagged prior to the 2022 surveys. To our knowledge, all tagged individuals used for the yearly estimates had an equal probability of resight, and marks should not have influenced the individual's

availability for resight. However, marked and unmarked detection rates among ungulates can change as a function of time since capture, relating back to the assumption of a closed population (Neal et al. 1993, Giudice et al. 2012, McCorquodale et al. 2013, Fieberg et al. 2015). Of the individuals we considered tagged and available for observation, we did not confirm the observation of 12 individuals during 2021 and 8 individuals during 2022, with 6 elk not uniquely identified during either year. It is possible a proportion of these elk were included in the analysis as the four unconfirmed tagged elk each year, or they were available for observation, but never observed because six different individuals missed during 2021 surveys were observed during 2022.

During the sampling periods of 2021 and 2022, seven elk were collared and/or tagged in Wise County, Virginia. These elk became established on a reclaimed mine from individuals that likely crossed the border from Kentucky into the protected VEMZ. However, we considered these tagged elk unavailable for observation during our sampling periods and excluded them from the analysis due to their location. If we had included these individuals in our estimates, we would have assumed that the proportion of marked to unmarked individuals was similar to that of the elk in Buchanan County.

An important component of the Lincoln-Petersen method is the that proportion of marked and unmarked individuals is consistent across the population (Otis et al. 1978). With this inference, every unobserved marked individual increases the population estimate proportional to the number of observed marked and unmarked individuals. However, it is possible this proportion was not consistent across our population. Although elk were tagged throughout Buchanan County, elk are herd animals, and all unobserved marked individuals could be a single group that went undetected during a survey, resulting in an overestimate of the population size.

We observed broad ranges for population estimates during surveys both years (Table 1) resulting in wide confidence intervals for our yearly estimates. Each year, we had one survey that likely underestimated the population size and one that likely overestimated (surveys 3 and 2 during 2021 and 4 and 1 during 2022, respectively; Table 1). Our study area is a mosaic of open reclaimed mines and dense forest cover (Lituma et al. 2021) that invariably caused us to miss elk groups. Also, because elk are heavily influenced by thermoregulatory needs (Demarchi and Bunnell 1993, Porter et al. 2002), our observations may have varied based on temperatures as elk can be less active and remain in vegetative cover at higher temperatures (Cook et al. 1998, Hinton et al. 2020). However, these conditions were minimized during our survey effort as we conducted surveys during crepuscular times during winter when elk should be most active (at the daily scale), most visible (due to

leaf-off conditions), and when thermoregulation is least important (due to cooler winter temperatures). Because of the potential for highly variable estimates, repeated surveys can reduce variation and provide more reliable assessments than single samples.

Although a Lincoln-Petersen index can be used as a quick abundance estimate with simple data collection and easily understood results, we suggest tagging efforts occur temporally closer to survey periods to avoid needing supplemental assumptions of marked individual availability for observation, tag retention, and survival. Additional repeated surveys can increase the robustness of the population estimate and reduce estimation variance. Many variables (e.g., precipitation, temperature, cover, and topography) can change the detectability of animals (Otten et al. 1993, Anderson et al. 1998) and have not been fully calibrated for survey efforts in the VEMZ yet. Nonetheless, our estimate of 303 individuals in 2022 indicates the Virginia elk population is on the trajectory of meeting the first goal in the 2019–2028 Virginia Elk Management Plan (VDWR 2019) of a viable elk population within the VEMZ.

Acknowledgments

We thank the Virginia Department of Wildlife Resources for project funding as well as their efforts releasing, capturing, collaring, and tagging all the elk used in our analysis. We also thank The Rocky Mountain Elk Foundation, The Nature Conservancy, and Southwest Virginia Sportsmen for their support for the restoration of elk in southwestern Virginia, and the Virginia Department of Transportation and private landowners for granting us access to their properties throughout this research.

Literature Cited

- Alt, G. L., C. R. McLaughlin, and K. H. Pollock. 1985. Ear tag loss by black bears in Pennsylvania. *Journal of Wildlife Management* 49:316–320.
- Anderson, C. R., Jr., D. S. Moody, B. L. Smith, F. G. Lindzey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. *Journal of Wildlife Management* 62:1055–1066.
- Bartmann, R. M., G. C. White, L. H. Carpenter, and R. A. Garrott. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. *Journal of Wildlife Management* 51:41–46.
- Beasom, S. L. and J. D. Burd. 1983. Retention and visibility of plastic ear tags on deer. *Journal of Wildlife Management* 47:1201–1203.
- Boulanger, J., J. Adamczewski, and T. Davison. 2018. Estimates of caribou herd size using post-calving surveys in the Northwest Territories and Nunavut, Canada: a meta-analysis. *Rangifer* 38:39–78.
- Braun, E. L. 1942. Forests of the Cumberland Mountains. *Ecological Monographs* 12:413–447.
- Brazier, R. E., A. Puttock, H. A. Graham, R. E. Auster, K. H. Davies, and C. M. L. Brown. 2021. Beaver: Nature's ecosystem engineers. *WIREs Water* 8:e1494.
- Carroll, C., M. K. Phillips, N. H. Schumaker, and D. W. Smith. 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. *Conservation Biology* 17:536–548.

- Chapagain, B. P. and N. C. Poudyal. 2020. Economic benefit of wildlife reintroduction: a case of elk hunting in Tennessee, USA. *Journal of Environmental Management* 269:110808.
- Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.
- Clark, J. B. 2012. The vascular flora of Breaks Interstate Park, Pike County, Kentucky, and Dickenson County, Virginia. Master's thesis, Eastern Kentucky University, Richmond.
- Conrad, J. M. 2009. Genetic variability, demography, and habitat selection in a reintroduced elk (*Cervus elaphus*) population. Doctoral dissertation, Kansas State University, Manhattan.
- Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in the summer and winter. *Wildlife Monographs* 141:3–61.
- Craighead, J. J., F. C. Craighead Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage herd as determined by biotelemetry. *Wildlife Monographs* 33:3–50.
- Curtis, P. D., B. Boldgiv, P. M. Mattison, and J. R. Boulanger. 2009. Estimating deer abundance in suburban areas with infrared-triggered cameras. *Human-Wildlife Conflicts* 3:116–128.
- Demarchi, M. W. and F. L. Bunnell. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). *Canadian Journal of Forest Research* 23:2419–2426.
- Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. *Journal of Wildlife Management* 50:660–663.
- Evans, S. B., L. D. Mech, P. J. White, and G. A. Sargeant. 2006. Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management* 70:1372–1378.
- Fieberg, J. R., K. Jenkins, S. McCorquodale, C. G. Rice, G. C. White, and K. White. 2015. Do capture and survey methods influence whether marked animals are representative of unmarked animals? *Wildlife Society Bulletin* 39:713–720.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- Giudice, J. H., J. R. Fieberg, and M. S. Lenarz. 2012. Spending degrees of freedom in a poor economy: a case study of building a sightability model for moose in northeastern Minnesota. *Journal of Wildlife Management* 76:75–87.
- Harestad, A. S. and F. L. Bunnell. 1979. Home range and body weight—a re-evaluation. *Ecology* 60:389–402.
- Hibbard, W. R., Jr. 1990. Virginia coal: an abridged history and complete data manual of Virginia coal production/consumption from 1748 to 1988. Virginia Center for Coal and Energy Research, Blacksburg.
- Hinton, J. W., A. E. Freeman, V. St-Louis, L. Cornicelli, and G. J. D'Angelo. 2020. Habitat selection by female elk during Minnesota's agricultural season. *Journal of Wildlife Management* 84:957–967.
- James, A. I. and D. J. Eldridge. 2007. Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biological Conservation* 138:351–359.
- Keller, B. J., R. A. Montgomery, H. R. Campa III, D. E. Beyer Jr., S. R. Winterstein, L. P. Hansen, and J. J. Millsaugh. 2015. A review of vital rates and cause-specific mortality of elk *Cervus elaphus* populations in eastern North America. *Mammal Review* 45:146–159.
- Larkin, J. L., R. A. Grimes, L. Cornicelli, J. J. Cox, and D. S. Maehr. 2001. Returning elk to Appalachia: foiling Murphy's Law. Pages 101–117 *in* D. S. Maehr, R. F. Noss, and J. L. Larkin, editors. Large mammal restoration: ecological and sociological challenges in the 21st century. Island Press, Washington, D.C.
- _____, D. S. Maehr, J. J. Cox, D. C. Bolin, and M. W. Wichrowski. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. *Journal of Wildlife Management* 67:467–476.
- Larter, N. C., A. R. E. Sinclair, T. Ellsworth, J. Nishi, and C. C. Gates. 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. *Animal Conservation* 4:299–309.
- Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular 118. U.S. Department of Agriculture, Washington, D.C.
- Lituma, C. M., J. J. Cox, S. F. Spear, J. W. Edwards, J. L. De La Cruz, L. I. Muller, and W. M. Ford. 2021. Terrestrial wildlife in the post-mined Appalachian landscape: status and opportunities. Pages 135–166 *in* C. E. Zipper and J. Skousen, editors. Appalachia's coal-mined landscapes. Springer, New York, New York.
- Lopez, R. R., N. J. Silvy, B. L. Pierce, P. A. Frank, M. T. Wilson, and K. M. Burke. 2004. Population density of the endangered Florida Key deer. *Journal of Wildlife Management* 68:570–575.
- McCorquodale, S. M., S. M. Knapp, M. A. Davison, J. S. Bohannon, C. D. Danilson, and W. C. Madsen. 2013. Mark-resight and sightability modeling of a western Washington elk population. *Journal of Wildlife Management* 77:359–371.
- McIntosh, T. E., R. C. Rosatte, J. Hamr, and D. L. Murray. 2009. Development of a sightability model for low-density elk populations in Ontario, Canada. *Journal of Wildlife Management* 73:580–585.
- Murie, O. 1951. The elk of North America. Stackpole Co., Harrisburg, Pennsylvania.
- Murrow, J. L., J. D. Clark, and E. K. Delozier. 2009. Demographics of an experimentally released population of elk in Great Smoky Mountains National Park. *Journal of Wildlife Management* 73:1261–1268.
- National Oceanic and Atmospheric Administration [NOAA]. 2022. Summary of monthly normals Grundy, VA 1991–2020. <<https://www.ncei.noaa.gov/products/land-based-station/us-climate-normals>>. Accessed 1 May 2022.
- Neal, A. K., G. C. White, R. B. Gill, D. F. Reed, and J. H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *Journal of Wildlife Management* 57:436–450.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:3–135.
- Otten, M. R. M., J. B. Haufler, S. R. Winterstein, and L. C. Bender. 1993. An aerial censusing procedure for elk in Michigan. *Wildlife Society Bulletin* 21:73–80.
- Pericak, A. A., C. J. Thomas, D. A. Kroodasma, M. F. Wasson, M. R. V. Ross, N. E. Clinton, D. J. Campagna, Y. Franklin, E. S. Bernhardt, and J. F. Amos. 2018. Mapping the yearly extent of surface coal mining in Central Appalachia using Landsat and Google Earth Engine. *PLOS One* 13: e0197758.
- Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 6:1–48.
- Popp, J. N., T. Toman, F. F. Mallory, and J. Hamr. 2014. A century of elk restoration in eastern North America. *Restoration Ecology* 22:723–730.
- Porter, W. P., J. L. Sabo, C. R. Tracy, O. J. Reichman, and N. Ramankutty. 2002. Physiology on a landscape scale: plant-animal interactions. *Integrative and Comparative Biology* 42:431–453.
- Powell, J. W. 1895. Physiographic regions of the United States. National Geographic Monographs, American Book Company, New York, New York.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Rivest, L., H. Crepeau, and S. Baillargeon. 2022. Caribou: Estimation of caribou abundance based on radio telemetry data. R package version 1.1-1.
- Roberts, C. W., B. L. Pierce, A. W. Braden, R. R. Lopez, N. J. Silvy, P. A. Frank, and D. Ransom Jr. 2006. Comparison of camera and road survey estimates for white-tailed deer. *Journal of Wildlife Management* 70:263–267.
- Seroussi, E., E. Yakobson, S. Garazi, Z. Oved, and I. Halachmi. 2011. Short communication: Long-term survival of flag eartags on an Israeli dairy farm. *Journal of Dairy Science* 94:5533–5535.
- Stadtmann, S. and P. J. Seddon. 2020. Release site selection: reintroductions and the habitat concept. *Oryx* 54:687–695.
- Virginia Department of Wildlife Resources [VDWR]. 2019. Virginia elk management plan, 2019–2028. Virginia Department of Wildlife Resources, Richmond.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494–499.