

Articles

Population Dynamics Model to Inform Harvest Management of a Small Elk Herd in Central New Mexico

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Abstract

Crop depredation by wildlife is a frequent concern for natural resource managers and mitigation of this issue is often an important task for wildlife agencies. Elk *Cervus elaphus* and other ungulate species have depredated corn *Zea mays* at Bosque del Apache National Wildlife Refuge, New Mexico, USA, interfering with the ability of the Refuge to provide sufficient supplemental nutrition to overwintering sandhill cranes *Antigone canadensis* and geese (Anatidae). We estimated annual adult survival and calf recruitment rates of elk from 2011 to 2013 at Bosque del Apache National Wildlife Refuge. Natural adult survival (excludes human-related mortalities) was high (mean = 98.3%; 95% CI = 95.0–100.0%). Calf recruitment was lower than in some populations, and ranged from 13.0 to 36.7 calves : 100 cows at time of recruitment (March and April) with a mean of 21.9 (SD =12.9). Using this information, we constructed a harvest management model to determine annual harvest quotas required to stabilize the growth of the elk herd on the Refuge. The female segment of the herd is growing at an annual rate of 9.0% (95% CI = -1.1–24.1%). To stabilize the growth rate of the female elk population, 8.0% (95% CI = -1.1–19.4%) of the cows would need to be harvested annually. We estimated an adult elk abundance of 40.0 (SE = 4.57; 95% CI = 33.8–52.6) in 2012 and 61.1 (SE = 7.21; 95% CI = 49.9–78.8) in 2013. Our harvest management model provides Refuge staff, who ultimately intend to improve corn yield, with valuable information needed to stabilize the elk herd. Further, our approach outlines a simple, easily implemented modeling technique that can be used for the management of other ungulate herds.

Keywords: age ratio; crop depredation; demographic stochasticity; hunting; mark–resight; sex ratio; temporal variation

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Introduction

Elk *Cervus elaphus* were extirpated from New Mexico by the early 20th century (New Mexico Department of Game and Fish [NMDGF] 2007). After extensive reintroduction efforts across New Mexico and population expansion, elk sightings at Bosque del Apache National Wildlife Refuge (hereafter, Refuge) began to occur in the early 2000s. This herd likely originated from the mountains to the west (U.S. Fish and Wildlife Service 2013) or from elsewhere within the Rio Grande Valley, and the level of immigration and emigration still occurring is unknown. Since colonization, the resident herd has increased and is contributing to crop depredation issues on the Refuge. Personnel have documented elk depredation on corn *Zea mays*, which is used as a supplemental food source for overwintering sandhill cranes *Antigone canadensis* and geese (Anatidae) at the Refuge, and in part to mitigate depredation on private croplands by migratory water birds (U.S. Fish and Wildlife Service 2013).

Crop damage by wildlife causes approximately US\$4.5 billion in losses/y in the United States (Conover 2002). New Mexico Department of Game and Fish (NMDGF) spends much time and money every year to reduce crop damage by wildlife, especially on irrigated croplands in river valleys (S.G. Liley, NMDGF, personal communication). Elk and other ungulate depredation of corn potentially interferes with the management strategy of the Refuge. For example, if an insufficient corn crop is produced, crop depredation on private lands by migratory water birds might increase, and Refuge managers could be forced to purchase additional supplemental feed or increase cultivated acres (A.A. Mertz, Bosque del Apache National Wildlife Refuge, personal communication). Among depredation issues on the Refuge, the U.S. Fish and Wildlife Service and the NMDGF do not want this elk herd expanding to private lands, which could result in social and economic impacts to neighboring farmers (J. Vradenburg, Bosque del Apache National Wildlife Refuge, personal communication; S.G. Liley, personal communication).

Elk eat approximately 2.5% of their body weight daily (Miller 2002), so an elk weighing 227 kg consumes 5.7 kg of dry matter/d. Even if corn is only a portion of the summer diet, elk could potentially consume substantial amounts of the crop. More importantly, if elk damage or consume the tassel (as was documented; DeVore 2014), no grain will form because the pollen source was removed (McWilliams et al. 1999). Thus, even relatively small numbers of elk could be detrimental to corn crops, especially if tassels are targeted.

Elk depredate corn on the Refuge, so we were interested in understanding the demographics of the resident herd to inform population and harvest management strategies (U.S. Fish and Wildlife Service 2013). Newly colonizing populations, such as the herd on the Refuge, have potential for high rates of increase (Caughley and Birch 1971). The four main aspects of population dynamics are births, immigration, deaths, and emigration (White 2000a). For reasons of simplicity,

immigration and emigration are often excluded from the assessment of population dynamics because of the difficulty of estimating these parameters. Consequently, birth and death rates are estimated to determine population growth, though the degree to which growth is biased depends upon the degree of movement in and out of the population (Hatter and Bergerud 1991; Skalski et al. 2005; DeCesare et al. 2012).

Annual adult elk survival is often high, especially when human-related mortalities are excluded (Ballard et al. 2000; Lubow and Smith 2004). This is typically the case for colonizing elk populations as well (Eberhardt et al. 1996; Bender and Piasecke 2010). Hunter harvest, a primary tool of elk management, is often the leading cause of mortality in hunted populations (Unsworth et al. 1993; Ballard et al. 2000; Stalling et al. 2002; Webb et al. 2011). Elk harvest, especially on adult females, can be implemented to reduce populations to a more desirable level. Managing adult survival through hunter harvest is likely more feasible than attempting to reduce calf recruitment directly.

Our research objectives were to estimate abundance and model population dynamics of the elk herd at Bosque del Apache National Wildlife Refuge to guide elk harvest management strategies. The results of this study will assist the Refuge in managing the elk herd and reducing crop depredation. Additionally, the model we developed can be parameterized with alternative recruitment and survival rates, which can enable other agencies to develop population management strategies for ungulate populations elsewhere.

Study area

Bosque del Apache National Wildlife Refuge is located in Socorro County, New Mexico, USA. It is situated at the lower end of the middle Rio Grande Valley (Post et al. 1998), approximately 13 km south of San Antonio, New Mexico, USA. The Refuge spans 23,162 ha (Taylor and McDaniel 1998), with approximately 6,000 ha of floodplain that consists of riparian forests, wetland impoundments, and cultivated crops (Zwank et al. 1997). The floodplain portion of the Refuge straddles the Rio Grande River for 20 km (Taylor and McDaniel 1998). Much of the floodplain on the west side of the river is utilized to produce crops and moist-soil plants (Thorn and Zwank 1993). The river valley has a mean width of 6 km (Taylor and McDaniel 1998) and lies at an elevation of approximately 1,375 m. The remainder of the Refuge consists of Chihuahuan desert scrub and semidesert grasslands (Brown 1982). Mountain ranges rise 1,600 m and 2,000 m to the east and west, respectively (Taylor and McDaniel 1998).

Elk on the Refuge primarily use the riparian corridor as their habitat (DeVore et al. 2016). Much of the riparian corridor on the Refuge is an intensively managed wetland system. A complex network of canals and drains transports water to management units (Post et al. 1998). The moist soil bottomlands on the Refuge are highly altered, with numerous roads, irrigation canals, and wetland and agricultural impoundments. The Refuge



manages for moist-soil plants and agricultural crops. Agriculture crops have included corn, alfalfa *Medicago sativa*, clover *Trifolium* spp., oats *Avena sativa*, barley *Hordeum vulgare*, and wheat *Triticum aestivum*, which provide supplemental food for migratory water birds or are used as cash crops for cooperative farmers (Zwank et al. 1997). At the time of this study, the primary crops were corn and alfalfa (DeVore 2014).

Methods

We developed a stochastic model of elk population dynamics based on recruitment and adult survival of the elk herd at the Refuge. We used this model to determine the magnitude of annual cow harvest at various population sizes that would be needed to maintain the population at a steady state (i.e., 0% population growth). We also used a mark–resight model and an aerial survey to estimate elk abundance. We used these results to assist the Refuge in managing the elk herd (i.e., harvest) and reducing crop depredation.

Capture

New Mexico Department of Game and Fish personnel captured elk to test for chronic wasting disease during winter 2010–2011 (Wild et al. 2002; Gordon et al. 2009). To collect samples, NMDGF personnel immobilized adult elk using helicopter-capture techniques (McCorquodale et al. 1988). During those captures, NMDGF personnel deployed very high frequency (VHF) radiocollars (MOD-500; Telonics, Inc., Mesa, AZ) and tags on captured elk to investigate the objectives of this study. The capture crew administered 3 mg carfentanil with 70 mg of xylazine or 10 mg A-3080 with 70 mg of xylazine via 1.5 mL Dan-Inject (Dan-Inject, Borkop, Denmark) darts and a Dan-Inject JM Special 25 dart gun; elk were reversed with Naltrexone and Yohimbine (K. Mower, NMDGF, personal communication). They placed an ear tag in the right ear of the elk captured in October 2010, while they placed one ear tag on each side of the collar (both tags with duplicate number) of elk captured in March 2011. Collars were equally deployed between groups of elk on the Refuge and sexes to create a mixture of marked and unmarked animals across the Refuge.

We captured additional elk using Clover traps (Clover 1956) from late January to early May 2012, and during March 2013. To lure elk into the traps, we used alfalfa hay, salt blocks, and anise extract. We restrained captured elk by hand using lariats, and blindfolded them once they were secured. We fitted females >1.5 y old with a satellite uplink global positioning system (GPS) collar (G2110E Iridium/GPS Location Collar; Advanced Telemetry Systems, Isanti, MN) or a VHF collar (Telonics MOD-500). Collars had an ear tag attached to each side of the collar (both tags with duplicate number). Global Positioning System collars transferred data via the Iridium satellite system, which emailed data daily. The GPS collars were equipped with VHF beacons that ran 8 h/d to facilitate mortality investigations and collar

retrieval. They also contained drop-off mechanisms and mortality switches. Radiocollars were equipped with drop-off mechanisms that were set for November 2013. We conducted this research under the approval of the Texas Tech University Animal Care and Use Committee (approval number T11085), NMDGF (authorization number 3355), and the National Wildlife Refuge System Research and Monitoring Special Use Permit (permit numbers B11F1, Bio12-03, and Bio13-03).

Management hunt and culling

The Refuge hosted a population management hunt for antlerless elk in February 2013 (U.S. Fish and Wildlife Service 2013). The NMDGF draw license system was used to select hunters who lived within a short driving distance of the Refuge and who did not receive a tag in the regular elk-permit drawing for the 2012–2013 New Mexico elk hunting season. The hunt consisted of seven consecutive 2-d intervals, with 2 hunters per interval. Refuge personnel escorted each hunter. The hunt was not considered a sport hunt, but designed to reduce elk abundance; therefore, elk project personnel provided recent location data of female groups to improve hunt success. Collared animals were off limits for harvest. We examined a sample of the harvested adult females to estimate a pregnancy rate (Program R function “binom.test”; Kanji 2006).

Adult survival

The VHF collars were not outfitted with mortality switches, so we plotted locations on a weekly basis to monitor mortality. We triangulated the location of VHF-collared elk ≥ 4 times/wk. Locations for each elk were spaced ≥ 12 h apart. When the error polygons of three consecutive locations overlapped, researchers investigated the fate of the individual. Global Positioning System collars indicated mortality status when the collar had been stationary for six consecutive hours. Personnel promptly investigated suspected deaths to determine the cause of mortality. If the date of death was unknown, we used the median date between the first and second overlapping mortality locations. To model adult survival, we used the Kaplan–Meier estimator with staggered entry because some animals were added via trapping and others were lost due to collar failure during the study (Pollock et al. 1989). We conducted survival analysis in R using the function “km” in the package “asbio” (R Core Team 2013; Aho 2017).

Calf recruitment and adult sex ratios

Calf survival and recruitment are important factors in elk population dynamics (Allee et al. 1949; Pimlott 1967; Gaillard et al. 2000; Raithel et al. 2007). The ratios of calves to cows (calves per 100 cows) can be used to estimate recruitment rates into the adult population. Adult sex ratios are also important demographic factors that could influence population dynamics. For instance, herds with too few mature bulls might exhibit calving



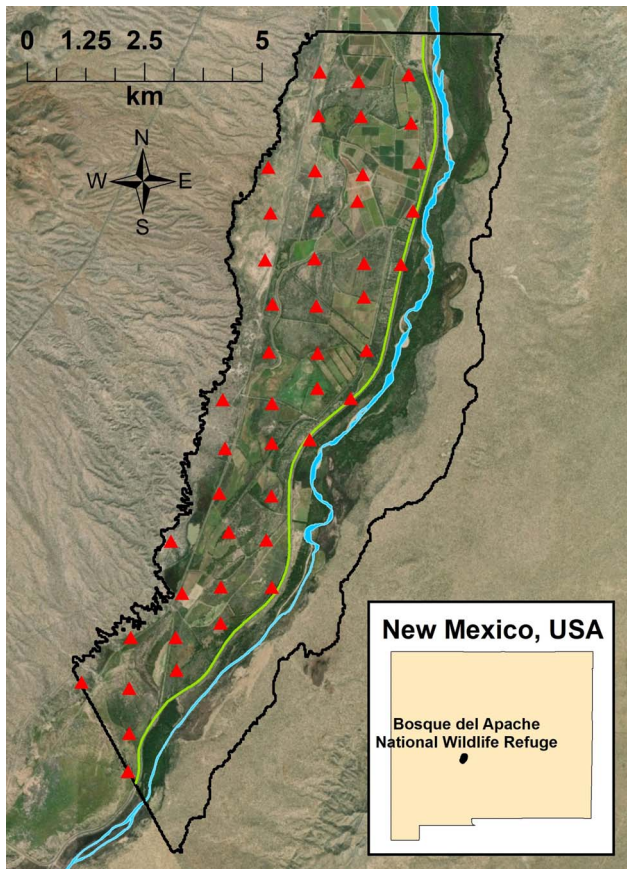


Figure 1. Locations of cameras (red triangles) during 2011–2013 across the study area (designated by black exterior line) at Bosque del Apache National Wildlife Refuge in central New Mexico, USA. The Rio Grande River (blue) transects the study area. The levy (green line) running along the low flow conveyance channel is the eastern boundary of the camera grid.

that is delayed and over a longer interval (Squibb et al. 1991; Noyes et al. 1996), which may reduce calf survival.

To estimate age and sex ratios, we deployed infrared motion-triggered cameras (Bushnell Trophy Cam, Overland Park, KS) on a grid of 1 × 1 km cells across the study area (Figure 1). This grid was composed of 47 cells and cameras were located along game trails, within 100 m of each cell center. To avoid cameras being destroyed during Rio Grande River flooding events, we did not place cameras east of the levy that runs along the low-flow conveyance channel (Figure 1). Camera height above the ground was approximately 0.75 m (Ford et al. 2009).

Elk calves are typically born from late May to early June. Using the grid of camera traps, we estimated calf : cow and bull : cow ratios from March and April 2011–2013. We excluded counts during May in each year because of the difficulty of distinguishing between calves and adult cows. During analysis, we excluded photos if one or more of the individuals in the photo could not be confidently identified to age or sex

(Jacobson et al. 1997; McCoy et al. 2011). Using photos from camera traps to estimate age- and sex-ratios assumes equal detection among the age- and sex-classes.

We estimated calf : cow ratios as

$$\hat{R}_{j/f} = j/f,$$

where j = the total number of calves observed and f = the total number of adult cows (≥ 1.5 y in age) observed. We used a single survey each year and sampled animals with replacement; therefore, we estimated the standard error (Skalski et al. 2005:56) as

$$SE(\hat{R}_{j/f}) = \sqrt{\frac{\hat{R}_{j/f}(1 + \hat{R}_{j/f})^2}{n}} = \sqrt{\frac{nj}{f^3}},$$

where n = the total number of calves and cows observed in the survey. We used the log-transformation to estimate confidence intervals (CI; Skalski et al. 2005:56)

$$CI = \left[\hat{R}_{j/f} e^{-z_{1-\frac{\alpha}{2}} \sqrt{\frac{\text{Var}(\hat{R}_{j/f})}{\hat{R}_{j/f}^2}}}, \hat{R}_{j/f} e^{z_{1-\frac{\alpha}{2}} \sqrt{\frac{\text{Var}(\hat{R}_{j/f})}{\hat{R}_{j/f}^2}}} \right].$$

to compare recruitment between years we used a 2-sample z-test (Kanji 2006).

We used the same equations to estimate standard errors and confidence intervals of the bull : cow ratios ($\hat{R}_{m/f}$) by replacing the number of calves (j) with the number of bulls (m). In addition, during clover trapping, which was conducted from late January to early May 2012, we determined the proportion of captured calves that were female (R function “binom.test”; Kanji 2006). This estimate only applies to 2012 because we did not capture any calves in 2013. We used an alpha level of 0.05 for all analyses.

In late February 2013, immediately prior to the camera sampling period for determining age and sex-ratios, a population management hunt was held on the Refuge for antlerless elk. This harvest reduced the number of adult females, and calves at this age (8–9 mo) likely survived without their mothers (Cook 2002; rumen is fully developed at 2 mo old); therefore, we adjusted the 2013 calf : cow ratio to account for increased cow mortality (Bender et al. 2002). We used Kaplan–Meier with staggered entry (Pollock et al. 1989) to estimate an adult female survival rate, incorporating only the mortalities of the marked females that were harvested during the hunt. We multiplied this adult female survival rate by the unadjusted 2013 calf : cow ratio

$$\hat{R}_{j/f,Adj} = \hat{S}_{f,Adj} \times \hat{R}_{j/f},$$

where $\hat{R}_{j/f,Adj}$ = the adjusted calf : cow ratio (recruitment rate), $\hat{S}_{f,Adj}$ = the adjusted adult female survival rate from August 2012 to August 2013, and $\hat{R}_{j/f}$ = the unadjusted calf : cow ratio in 2013. We used the delta method to estimate variance for the 2013 adjusted calf : cow ratio

$(\widehat{\text{var}}_{\hat{R}_{j/f,Adj}})$; under the assumption that the survival rate and unadjusted ratio were independent; Powell 2007)

$$\widehat{\text{var}}_{\hat{R}_{j/f,Adj}} = \left(\widehat{\text{var}}_{\hat{S}_{f,Adj}} \times \hat{R}_{j/f}^2\right) + \left(\widehat{\text{var}}_{\hat{R}_{j/f}} \times \hat{S}_{f,Adj}^2\right).$$

Population dynamics

We modeled the annual growth rate of this elk population with a simple model representing the female segment of the population (Hatter and Bergerud 1991; White and Bartmann 1997; Bender and Piaseke 2010; DeCesare et al. 2012; see Supplemental R Code in Text S1, *Supplemental Material*). Annual growth rate (λ) of the female segment of the population was estimated as

$$\lambda = \hat{S} \times \left(1 + \left(\hat{R} \times c\right)\right),$$

where \hat{S} = adult survival, \hat{R} = the calf : cow ratio at recruitment, and c = the proportion of recruited calves that were female (Hatter and Bergerud 1991; DeCesare et al. 2012). Recruitment estimates contained different sample sizes each year, so we weighted the mean recruitment rate by the variances (see below).

We only estimated the growth of female segment of the herd; therefore, we multiplied the recruitment rate by the proportion of recruited calves that were female (c ; DeCesare et al. 2012). We did not estimate the calf sex ratio at time of recruitment because of the difficulty in distinguishing between sexes with cameras. Instead, we incorporated a female calf proportion of 0.5 into the population model, assuming parity. However, calf sex ratios could be skewed (Kohlmann 1999), so we also ran the model using female proportions of 0.45, 0.55, and 0.60 to determine its effect on λ . We characterized the uncertainty in the estimates of growth rate using a parametric bootstrap (White 2000b).

To inform culling of the elk herd for population control (i.e., stable population, $\lambda = 1$), we incorporated elk harvest into the model,

$$1 = \hat{S} \times \left(1 + \left(\hat{R} \times c\right)\right) \times (1 - g)$$

where g = the proportion of the population that needs to be harvested (i.e., harvest rate) to maintain stable population growth. After some rearranging, we estimated g as

$$g = 1 - \frac{1}{\hat{S} \times \left(1 + \left(\hat{R} \times c\right)\right)}.$$

We characterized the uncertainty in the harvest rate estimates using a parametric bootstrap (White 2000b).

The parameters of our model contain uncertainty associated with their estimated values. Ignoring some components of uncertainty can result in misleading inferences (Calder et al. 2003; McGowan et al. 2011). To improve model inference, and subsequent decisions made from them, we incorporated much of this

uncertainty into the population model (McGowan et al. 2011). We integrated demographic stochasticity, temporal variation, and parametric uncertainty into the parameter values. Demographic stochasticity is the change in population demographics due to random chance; it is “essentially the same as the randomness that causes variation in the numbers of heads and tails you get if you repeatedly flip a coin” (Morris and Doak 2002:22). For example, if an experiment of flipping 20 coins (i.e., individuals) with 0.5 probability of getting a head (i.e., surviving) was repeated multiple times, it would result in 10 heads (i.e., individuals living) 17.6% of the time, 11 heads 16.0% of the time, 12 heads 12.0% of the time, etc., if the process was binomially distributed. Temporal variation is the fluctuations in demographics over time due to environmental or other changes (Morris and Doak 2002; McGowan et al. 2011). Parametric uncertainty is the uncertainty of parameter estimates that arises from sampling variation and sampling error (White 2000b; McGowan et al. 2011).

We incorporated temporal variability by allowing adult survival to follow a beta distribution

$$\hat{S} \sim \text{BETA}(\hat{\alpha}, \hat{\beta}).$$

The shape parameters of the beta distribution were estimated using the method of moments (Morris and Doak 2002) so that

$$\hat{\alpha} = \frac{\hat{S}^2 \times (1 - \hat{S})}{\widehat{\text{var}}(\hat{S})} - \hat{S}$$

and

$$\hat{\beta} = \frac{\hat{S} \times (1 - \hat{S})^2}{\widehat{\text{var}}(\hat{S})} - (1 - \hat{S}),$$

where \hat{S} = the estimated mean annual adult survival probability and $\widehat{\text{var}}(\hat{S})$ = the estimated variance of the mean annual adult survival probability. The adult survival estimate also contained parametric uncertainty, but we could not separate parametric uncertainty from the temporal variability because survival was monitored for only 2 y.

We assumed the proportion of calves that were female was 0.45, 0.50, 0.55, and 0.60 and was normally distributed with a variance of 0.01. We estimated the total variance of recruitment ($\widehat{\text{var}}_{\text{Tot}}(\hat{R})$) by combining its sampling variance and temporal variance. We estimated the total variance of recruitment as

$$\widehat{\text{var}}_{\text{Tot}}(\hat{R}) = \sigma_T^2 + \frac{\sum \widehat{\text{var}}(\hat{R}_i)}{n},$$

where \hat{R}_i = the estimated recruitment each year and i = year. We estimated \hat{R} as a weighted mean, to account for

heterogeneous variances, as

$$\hat{R} = \frac{\sum \hat{w}_i \times \hat{R}}{\sum \hat{w}_i}$$

where \hat{w}_i = the weight. We estimated \hat{w}_i as

$$\hat{w}_i = \frac{1}{\sigma_T^2 + \widehat{\text{var}}(\hat{R}_i)},$$

where σ_T^2 = the temporal variation of recruitment estimated by the variance discounting method and $\widehat{\text{var}}(\hat{R}_i)$ = the mean of sampling variances (White 2000b). We used the function “uniroot” in Program R (R Core Team 2013) because the above equations must be evaluated iteratively to solve for temporal variation (see uniroot function in in Text S1, *Supplemental Material*; White 2000b). We incorporated the total variance of recruitment into the model and assumed it followed a beta distribution

$$\hat{R} \sim \text{BETA}(\hat{\gamma}, \hat{\delta}),$$

where

$$\hat{\gamma} = \frac{\hat{R}^2 \times (1 - \hat{R})}{\widehat{\text{var}}_{\text{Tot}}(\hat{R})} - \hat{R}$$

and

$$\hat{\delta} = \frac{\hat{R} \times (1 - \hat{R})^2}{\widehat{\text{var}}_{\text{Tot}}(\hat{R})} - (1 - \hat{R}).$$

We incorporated demographic stochasticity into adult survival and recruitment using a binomial distribution when estimating the number of females to harvest given initial population sizes. We estimated the number of adult females surviving an interval (N_{Surv}) as

$$N_{\text{Surv}} \sim \text{BINOM}(N_F, \hat{S}),$$

where N_F = an initial number of adult females in a population (i.e., 10–60 individuals). We then assumed

$$N_{\text{Recruit}} \sim \text{BINOM}(N_{\text{Surv}}, (\hat{R} \times c)),$$

where N_{Recruit} = number of female calves recruited into the adult population. This allowed us to estimate the number of females to harvest (N_{Harvest}) as

$$N_{\text{Harvest}} \sim (N_{\text{Surv}} + N_{\text{Recruit}}) - N_F$$

and account for demographic stochasticity, temporal variation, and parametric uncertainty (McGowan et al. 2011; see Supplemental R Code in Text S1, *Supplemental Material*).

Abundance

Mark–resight surveys were conducted in January of each year (2012 and 2013) to provide abundance

estimates prior to recruitment of calves and hunting. We considered each day in which elk were observed during our regular elk research activities as a secondary survey occasion. We were not always able to uniquely identify all marked individuals. When this occurred, sampling without replacement within secondary survey occasions is assumed (McClintock et al. 2009; McClintock and White 2009).

We used the mixed logit-normal mark–resight model in Program MARK to estimate adult elk abundance (McClintock et al. 2009; McClintock and White 2009). We examined 4 models (logit link function) for each year. We modeled resighting probability as a constant ($p(.)$), a linear trend ($p(\text{Trend})$), a quadratic trend ($p(\text{Trend}^2)$), or as survey-occasion-specific ($p(t)$). To evaluate each model’s support, we used Akaike’s Information Criterion corrected for small sample size (AIC_c ; Anderson 2008; Arnold 2010). We considered models competitive if $\Delta\text{AIC}_c < 2.0$ (Burnham and Anderson 2002; Anderson 2008).

A helicopter survey was conducted by NMDGF across the Refuge on 9 October 2011. Transects were 250 m wide on each side of the helicopter, spaced 500 m apart, and were flown 50 m above the ground at 100 km/h ground speed. Personnel recorded the age, sex, and marking status of elk groups. We used the bias-adjusted form of the Lincoln–Petersen estimator to estimate the abundance (\hat{N}) of adult elk (>1 y old; Chapman 1951; Williams et al. 2002)

$$\hat{N} = \frac{(n_1 + 1) \times (n_2 + 1)}{(m_2 + 1)} - 1$$

where n_1 = the number of marked elk in the herd, n_2 = the total number of elk sighted during the survey (includes both marked and unmarked individuals), and m_2 = the number of marked elk seen during the survey. We estimated variance ($\widehat{\text{var}}(\hat{N})$; Seber 1970; Williams et al. 2002) as

$$\widehat{\text{var}}(\hat{N}) = \frac{(n_1 + 1) \times (n_2 + 1) \times (n_1 - m_2) \times (n_2 - m_2)}{(m_2 + 1)^2 \times (m_2 + 2)}.$$

We estimated the 95% confidence interval (Rexstad and Burnham 1991) as

$$\text{CI} = \left[\frac{n_1 + (N - n_1)}{\left(z_{1-\frac{\alpha}{2}} \times \sqrt{\frac{\log(1 + \widehat{\text{var}}(\hat{N}))}{(N - n_1)^2}} \right)}, n_1 + (N - n_1) \times e^{\left(z_{1-\frac{\alpha}{2}} \times \sqrt{\frac{\log(1 + \widehat{\text{var}}(\hat{N}))}{(N - n_1)^2}} \right)} \right].$$

Results

Capture

The NMDGF captured and radiocollared (VHF) 28 elk (13 males, 15 females) during October 2010 ($n = 13$) and March 2011 ($n = 15$) via darting from a helicopter. We trapped for approximately 620 total clover-trap nights during 2 periods; circa 28 January 2012–1 May 2012, and

Table 1. Annual recruitment rates (calves : 100 cows) and spring adult sex ratios (bulls : 100 cows) of elk *Cervus elaphus* at Bosque del Apache National Wildlife Refuge, New Mexico, USA, from March and April 2011–2013.

Year ^a	Ratio type	n ^b	Ratio	SE	Lower 95% CI	Upper 95% CI
2011	Calf : cow	539	13.04	1.59	10.26	16.56
	Bull : cow	737	48.71	3.53	42.27	56.14
2012	Calf : cow	624	36.73	3.02	31.26	43.15
	Bull : cow	775	56.91	4.03	49.54	65.38
2013	Calf : cow	440	16.17 ^c	2.98	11.27	23.19

^a Recruitment for 2013 was adjusted for female harvest prior to the sampling period (Bender et al. 2002). The 2013 bull : cow ratio was not estimated because harvest and culling occurred prior to and during the sampling period.

^b The number of photos containing calves and/or cows for calf : cow ratios, and the number of photos containing bulls and/or cows for bull : cow ratios.

^c The 2013 unadjusted ratio was 22.6 calves : 100 cows.

circa 16–26 March 2013. We deployed 14 collars on females (11 GPS, 3 VHF). Five of the GPS collars we deployed were on females that were previously marked with a VHF collar. We captured 45 total elk using clover traps, and released female calves and all males without marking them. Ten of the 17 (58.8%; SE = 11.9%; 95% CI = 33.5–80.6%) calves we captured using clover traps from late January to early May 2012 were females, which did not differ from 50:50 ($P = 0.629$).

Management hunt and culling

From 15 to 28 February 2013 the Refuge hosted a population management hunt for antlerless elk. Thirteen rifle tags were issued, of which 10 hunters (76.9%) successfully harvested elk (9 adult females, 1 female calf). All of the adult females that were checked for pregnancy ($n = 8$; presence of a fetus) were pregnant (100%; 95% CI = 0.631–1.000). Although collared animals were off limits for harvest, 6 of the 10 harvested females were collared (5 VHF, 1 GPS); the difficulty of distinguishing between collared and uncollared animals contributed to this bias. Refuge staff culled a total of 10 elk, including 2 bulls in March 2013, 5 bulls and 1 cow in April 2013, and 2 yearling cows in July 2013.

Adult survival

We included 35 and 34 adult elk in the first and second years of survival analysis, respectively; specific individuals varied because some left the sample (e.g., mortality, collar failure, etc.), while we added others by trapping (Data S1, *Supplemental Material*). We marked 17 individuals at the start of the study period which survived both years. In total, we tracked 36 unique individuals (12 males, 24 females).

Eight adult mortalities (1 male, 7 females) occurred from our collared sample (Data S1, *Supplemental Material*). One female mortality was from unknown causes, but was not human-related. The remaining seven mortalities were hunting-related, which included one male that was legally harvested (sport) off of the study site (~47 km west of the Refuge) and six females harvested during the population management hunt on the Refuge. Thus, seven of eight included mortalities

were due to hunting (87.5%; SE = 11.7%; Data S1, *Supplemental Material*).

The average annual adult mortality rate from sport harvest (legally harvested male off-Refuge) was 0.017 (SE = 0.017; 95% CI = 0.000–0.051). Adult mortality from August 2012 to August 2013 due to population management harvest was 0.286 (SE = 0.102; 95% CI = 0.086–0.486). Natural adult survival (excludes human-related mortalities) was high, with an average annual rate of 0.983 (SE = 0.017; 95% CI = 0.950–1.017). We pooled years and sexes when hunting was excluded because only one nonhunting mortality occurred during the study period.

Calf recruitment and adult sex ratios

Recruitment of calves into the adult population ranged from 13.0 calves : 100 cows in March–April 2011 to 36.7 calves : 100 cows in March–April 2012 (Table 1; Data S2, *Supplemental Material*), with a weighted average of 21.9 calves : 100 cows (SD = 12.9). The nonweighted mean was similar at 22.0 calves : 100 cows, indicating relatively homogenous variances. Calf : cow ratios were different between all years ($z < -19.9$, $P < 0.001$). As a result of the harvest of cows during the management hunt immediately prior to the sampling period in 2013, we adjusted the calf : cow ratio to account for differential cow survival from August 2012 to August 2013 compared with the previous year. This adjustment was made using an adult survival rate based only on females and only included mortalities due to harvest during the management hunt, which was 0.714 (SE = 0.102; 95% CI = 0.514–0.914). Adult sex ratios were near 50 bulls : 100 cows in 2011 and 2012 (Table 1; Data S2, *Supplemental Material*). As a result of the culling of adults that occurred prior to and throughout the sampling period in March–April 2013, we were unable to provide an estimate of the adult sex ratio for 2013 that was unaffected by elk removal.

Population dynamics

Given average natural adult survival and recruitment with a 50:50 calf sex ratio, the female segment of this population is growing at a mean annual rate of 9.0% (SE = 6.6%; 95% CI = -1.1–24.1%; Table 2). The average



Table 2. Mean annual growth rates (λ) of the female segment of the elk *Cervus elaphus* herd and number of females to harvest given an initial population size of 30 females to maintain a stable population at Bosque del Apache National Wildlife Refuge, New Mexico, USA. Estimates are based on four calf sex ratios (female : male), and either include the 2013 adjusted recruitment estimate or exclude it altogether. The adult survival rate of 0.983 only includes natural mortality, whereas the survival rate of 0.966 includes natural and sport-harvest mortality (i.e., excludes management hunt and culling mortalities).

Adult survival	Calf sex ratio	λ			No. to harvest		
		Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Includes 2013 calf recruitment							
0.966	0.45	1.061	0.958	1.198	1.64	-1.30	4.97
	0.50	1.072	0.962	1.223	1.90	-1.20	5.46
	0.55	1.082	0.964	1.247	2.16	-1.13	5.95
	0.60	1.093	0.967	1.272	2.41	-1.01	6.42
0.983	0.45	1.080	0.986	1.216	2.14	-0.42	5.32
	0.50	1.090	0.989	1.241	2.39	-0.34	5.82
	0.55	1.102	0.992	1.265	2.65	-0.25	6.29
	0.60	1.112	0.994	1.291	2.90	-0.18	6.77
Excludes 2013 calf recruitment							
0.966	0.45	1.074	0.954	1.251	1.92	-1.44	6.01
	0.50	1.086	0.956	1.281	2.20	-1.38	6.59
	0.55	1.098	0.959	1.310	2.48	-1.27	7.11
	0.60	1.110	0.962	1.343	2.75	-1.19	7.66
0.983	0.45	1.093	0.981	1.270	2.42	-0.58	6.38
	0.50	1.105	0.984	1.300	2.70	-0.49	6.92
	0.55	1.117	0.985	1.331	2.96	-0.45	7.46
	0.60	1.129	0.988	1.364	3.24	-0.36	8.01

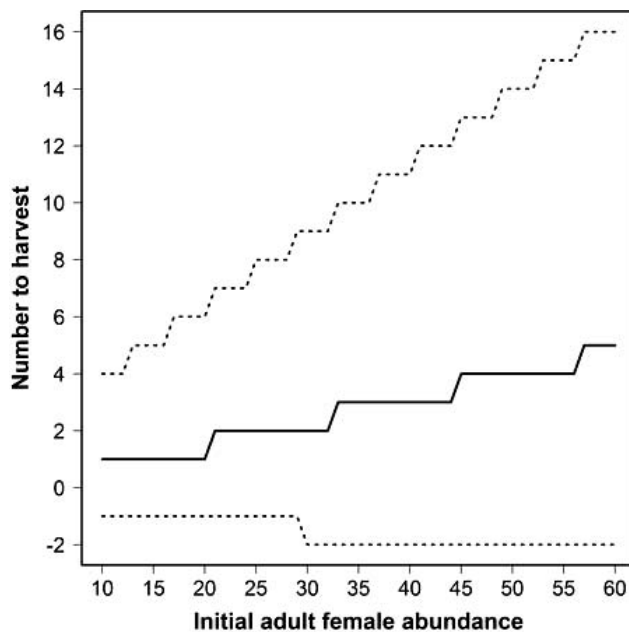


Figure 2. Estimated number of adult female elk *Cervus elaphus* to harvest to maintain zero population growth given initial adult female population sizes at Bosque del Apache National Wildlife Refuge in central New Mexico, USA; estimates based on demographic parameters from 2011–2013. Thick line represents the median and dotted lines represent the 95% confidence interval. Estimated using an annual adult survival of 0.983 and a 50:50 calf sex ratio.

proportion of cows required to be harvested to maintain a stable population (g) is 8.0% (SE = 5.4; 95% CI = -1.1–19.4%). When adult female abundance is 21–32, 2 females would need to be harvested annually to maintain a stable female population given demographic stochasticity, temporal variation, and parametric uncertainty (Figure 2). Changes in calf sex ratios do not appear to alter the herd growth rate (Table 2). If the recruitment rate from 2013 is excluded, the female segment of this population would be expected to grow at a mean annual rate of 10.5% (SE = 8.5%; 95% CI = -1.6–30.0%).

Abundance

We observed elk on 11 d during January 2012 (27–28 elk available for resighting; Data S3, *Supplemental Material*) and 15 d during January 2013 (30–31 elk available for resighting; Data S3, *Supplemental Material*). We estimated an adult elk abundance of 40.0 (SE = 4.57; 95% CI = 33.8–52.6) in 2012 and 61.1 (SE = 7.21; 95% CI = 49.9–78.8) in 2013 (Table 3) using the mixed logit-normal mark-resight model estimator. Comparisons of potential abundance estimators using AIC_c indicate the most competitive model was a quadratic trend in resighting probability during 2012 and a survey-occasion-specific resighting probability during 2013. We did not model-average because only the most competitive model each year had a $\Delta AIC_c < 2.0$ (Table 3). During the helicopter survey in 2011, NMDGF personnel observed 30 total elk (23 adults, 7 calves), of which 14 were marked adults. Twenty seven marked elk were in our sample at the time of the survey. We estimated 43.8 adults (SE = 4.67; 95% CI = 40.6–47.7) for October 2011.

Table 3. Mark–resight models and adult elk *Cervus elaphus* abundance estimates at Bosque del Apache National Wildlife Refuge, New Mexico, USA, during January 2012 and January 2013. For each model, $-2 \times \log$ -likelihood ($-2LL$), number of parameters (K), second-order Akaike's Information Criterion (AIC_c), difference in AIC_c compared with lowest AIC_c of the model set (ΔAIC_c), and AIC_c weight (w) are given.

Model ^a	-2LL	AIC _c	ΔAIC _c	w	K	Abundance			
						Mean	SE	Lower 95% CI	Upper 95% CI
2012									
p(Trend ²)	186.057	196.261	0.000	0.939	5	40.0	4.57	33.8	52.6
p(t)	179.636	202.556	6.295	0.040	11	32.0	1.43	30.0	35.9
p(.)	198.873	204.954	8.693	0.012	3	40.0	4.60	33.8	52.8
p(Trend)	197.495	205.631	9.370	0.009	4	40.0	4.59	33.8	52.7
2013									
p(t)	144.611	167.204	0.000	0.999	11	61.1	7.21	49.9	78.8
p(Trend)	174.205	182.294	15.089	0.001	4	61.1	7.28	49.9	79.0
p(.)	177.167	183.220	16.015	0.000	3	61.3	7.27	50.1	79.2
p(Trend ²)	173.366	183.499	16.294	0.000	5	61.1	7.28	49.8	79.0

^a Resighting probability was modeled as a constant (p(.)), a linear trend (p(Trend)), a quadratic trend (p(Trend²)), or as survey-occasion-specific (p(t)).

Discussion

The management goal of the Refuge is to produce 1.5 million pounds of corn/y to provide supplemental nutrition for overwintering sandhill cranes and other waterbirds (U.S. Fish and Wildlife Service 2013). However, as of December 2014, the Refuge has not met its corn yield goal since 2004 (A.A. Mertz, personal communication). Based on the professional opinion of local biologists (J. Vradenburg and A.A. Mertz, personal communication), it appeared elk were responsible for a considerable proportion of corn damage, which was one of the factors that inhibited the Refuge from producing adequate corn yields.

Given the results of our population modeling, 8.0% of females would need to be harvested annually to maintain the female segment of this population at a steady state. If recruitment of calves is uniform between sexes, a similar proportion of bulls would need to be harvested to maintain the male segment of the population at a steady state. However, our population model does not include estimates of immigration and emigration. If there is a net change in the growth rate of this elk herd due to these parameters, the estimated level of harvest required to maintain this population at a steady state will be biased (low if immigration is occurring and high if emigration is occurring). This is a newly colonized population, so immigration from outside the Refuge is likely occurring. Given immigration, our harvest recommendations are likely conservative (i.e., biased low) for maintaining a steady state and likely reduces the potential for overharvest.

We directly estimated adult survival and recruitment rates for the Refuge elk herd to parameterize our population model. However, we did not estimate calf sex ratios via camera-trapping at the time of recruitment (March and April) because of the difficulty of distinguishing between sexes of calves in photographs. Disparate sex ratios of calves might alter growth of the female segment of the population to some extent (Medin and Anderson 1979). Two herds in northern New Mexico (Bernal 2013; N.M. Tatman, NMDGF,

personal communication), as well as a herd in Yellowstone National Park (Barber-Meyer et al. 2008), exhibited calf sex ratios at birth that were not different from parity (although the ratios were skewed toward males in one year for Bernal [2013] and toward females in one year for Barber-Meyer et al. [2008]). However, Kohlmann (1999) found skewed calf sex ratios were associated with maternal condition. Ten of the 17 (58.8%; SE = 11.9%; 95% CI = 33.5–80.6%) calves we captured using clover traps from late January to early May 2012 were females, which did not differ from 50:50 ($P = 0.629$). This estimate has small sample size and could be biased if capture rates are dissimilar between sexes. Without a more robust sample size, the input values for the calf sex ratio in our population model could be biased. Therefore, we used four different calf sex ratios in our model to determine the effect this parameter has on population growth (Table 2). Population growth rates were similar among the various calf sex-ratio values. Thus, even if calf sex ratios at time of recruitment are slightly skewed from parity, estimated harvest rates by sex will remain relatively unbiased.

Our estimates of calf : cow ratios could be biased as a result of unequal detection of the age classes. However, we suspect little difference in the detection probabilities in photographs among cows and calves because they are typically grouped together during the March–April period during which we conducted camera-trapping and ratio estimation. Furthermore, we found similar calf : cow ratios for the study population across two different observation platforms. Unpublished data on age-classes obtained during our mark–resight surveys resulted in similar ratios obtained from camera-trapping (we chose to use the camera-based ratio estimates because their precision was better). The camera-based ratios were 13.0, 36.7, and 16.2 calves : 100 cows for 2011, 2012, and 2013 respectively, and the ratios obtained from the mark–resight surveys were quite similar at 20.5, 30.3, and 16.9 calves : 100 cows for 2011, 2012, and 2013 respectively.

Natural adult survival is high and fairly constant, whereas calf recruitment was highly variable. This is similar to what Gaillard et al. (1998, 2000) found in a

Table 4. Mean annual recruitment rates (calves : 100 cows) of Rocky Mountain elk *Cervus elaphus nelsoni* from across western North America.

Location	Years	Months	Ratio	Range	Source
Current study	2011	March–April	13.0	—	DeVore (2014)
Current study	2012	March–April	36.7	—	DeVore (2014)
Current study	2013	March–April	16.2	—	DeVore (2014)
Utah	1970–1972	January	55.7	39.0–68.0	Follis and Spillet (1974)
Michigan	1991–1992	April	48.6	48.4–48.8	Bender et al. (2002)
Alberta, Canada ^a	1998–1999	April	27.4	—	Hebblewhite et al. (2005)
Alberta, Canada ^b	1998–1999	April	14.6	—	Hebblewhite et al. (2005)
Oregon	2007–2009	February–April	26.3 ^c	25.0–28.0 ^c	Oregon Department of Fish and Wildlife (2009)

^a Area of low wolf *Canis lupus* density.

^b Area of high wolf density.

^c Average across herd units.

review of multiple studies of large herbivores. Raithel et al. (2007) estimated that 75% of variation in population growth of an elk herd in Montana was attributed to calf survival. Even though calf survival has relatively low elasticity compared with adult survival, it often has a larger effect on growth rates of populations because of its high variability (Gaillard et al. 2000; Raithel et al. 2007).

Recruitment of calves into the adult population varied substantially between years (13.0–36.7:100 cows; Tables 1 and 4) and exhibited a mean of 21.9 calves : 100 cows (SD = 12.9). The average is <30; therefore, this herd is relatively unproductive (Wisdom and Cook 2000). Recruitment rates, especially in 2011 and 2013, were lower than in some other elk populations (Follis and Spillet 1974; Bender et al. 2002; Table 4). The average recruitment rate across years in our study was comparable to those found by Hebblewhite et al. (2005) in areas with few wolves *Canis lupus*, and our 2011 and 2013 estimates were similar to their ratios in regions of high wolf populations. Average recruitment in our study was also similar to Rocky Mountain elk in Oregon from 2007 to 2009 (Oregon Department of Fish and Wildlife 2009).

Pregnancy rates of ≥ 2 -y-old females are typically between 80 and 100%, and yearling females could also conceive, though at a lower rate (Kittams 1953; Greer 1966; Follis and Spillet 1974; Eberhardt et al. 1996; Bender et al. 2002; Bender and Piasecke 2010). Although we only sampled eight adult females, all of them were pregnant. Fetal mortality is uncommon in elk unless severe undernourishment occurs (Thorne et al. 1976; Kozak et al. 1994), which was unlikely in the Refuge herd because of mild winters and abundant native and agriculture foods. If our assumptions of high pregnancy rates and low intrauterine mortality are correct, it is likely that mortality occurring after birth is the major regulating factor for juvenile recruitment at the Refuge.

Potential predators on the Refuge include mountain lions *Puma concolor* and coyotes *Canis latrans*; black bears *Ursus americanus* have also been sighted, although rarely. A concurrent study suggests mountain lion predation is a significant cause of mortality in elk calves at the Refuge (T.W. Perry, Furman University, personal communication). Additionally, during the past four summers Refuge personnel have observed calves that were blind. Oftentimes the blind calves were alone in open areas during the middle of the day. The Refuge had

some of those calves tested, but results were inconclusive. We do not know whether some of the calves regained sight and survived, or if they died. However, it is likely that many of the calves that exhibited these symptoms had low chances of survival because of their predisposition to predation, injury, and starvation.

During the population management hunt (antlerless only), 76.9% (10 of 13; SD = 0.117; 95% CI = 0.462–0.950) of hunters harvested elk. This is a much higher success rate than during regular hunting seasons for antlerless elk in New Mexico (NMDGF 2013). However, road access is extensive, elk were previously not hunted on the Refuge, and project personnel provided recent location data to hunter escorts because it was not a sport hunt. These factors likely increased harvest success on the Refuge. In the future, harvest success could decline as a result of lack of location information and elk response to hunting. Therefore, we suggest that Refuge staff track harvest success over time to better estimate the number of tags to allocate to meet harvest goals.

Management Implications

If the Refuge desires to maintain the elk herd at stable levels, our results indicate harvest will need to be a regular and integral part of management. Hunting is a significant element in managing most elk populations (Stalling et al. 2002). Hunting generates significant income for state game agencies, provides recreational opportunity for sportsmen (Bunnell et al. 2002), and is one of the main goals of the National Wildlife Refuge System (Fischman 2003). From the population management hunt alone, elk survival at the Refuge was markedly reduced compared with natural survival. In addition, 10 more elk were culled following the management hunt. We suggest that the Refuge determine a population level at which they are willing to sustain this herd. Through harvest or culling they can attempt to reduce the herd to such a level. Our population model then could be used to determine the magnitude of harvest required to maintain the population at a steady state.

Monitoring and evaluating management actions are important components of an adaptive management strategy, which is essential to making sound conservation decisions (Franklin et al. 2007). Adult survival was



high and stable, which is similar in many other elk herds, and it would be costly and invasive to directly estimate adult survival on a continual basis. Harvest success could vary through time, and calf recruitment is highly variable and has the greatest impact on population growth; therefore, we believe continued monitoring of these parameters will improve the effectiveness of management of this population. Other important factors to monitor might include success of various hunt strategies (e.g., number of hunters/time frame, time of year), corn yields, crop depredation due to wildlife (i.e., species-specific damage), and elk abundance. Monitoring and evaluating these factors will assist the Refuge in evaluating the success of their elk harvest program and allow them to more effectively adjust management actions as conditions change through time.

On account of uncertainty in our model, implementation of recommended harvest could inflate the risk of extirpating this population. In addition to the number of elk harvested, some wounding loss could contribute to the removal of animals (Unsworth et al. 1993), and might even account for a substantial portion of mortality (Leptich and Zager 1991). However, risk of extirpation is mitigated by the abundance of other elk herds within relatively close proximity, such as in the Rio Grande Valley and surrounding mountain ranges. Also, harvest success will likely decline at low population sizes. Although this elk population has caused crop depredation issues, regulation of the herd will provide increased opportunities for hunters, photographers, wildlife viewers, environmental education and interpretation at the Refuge.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Data describing elk *Cervus elaphus* survival over a 2-y period (August 2011–July 2013) at Bosque del Apache National Wildlife Refuge, New Mexico, are contained in a tab-delimited text file (survival_data.txt). This file contains 9 columns and 69 records. The ‘Elk_ID’ column contains a unique identifier for each elk. The ‘Sex’ column identifies the sex of each elk. The ‘Year’ column contains a 1 or 2 as indicators of year. The ‘Start Date’ and ‘Start Day’ columns contain the date or day of the year in which the elk entered the sample, respectively. The ‘End Date’ and ‘End Day’ columns contain the date or day of the year in which the elk exited the sample, respectively. The ‘Event’ column indicates natural mortality as 1 and survival as 0. The ‘Cause’ column is a comment field with descriptions of mortality causes.

Found at DOI: <https://doi.org/10.3996/012018-JFWM-008.S1> (4 KB TXT).

Data S2. Elk *Cervus elaphus* counts by age- and sex-class obtained from camera-trapping images (March and

April 2011–2013) from Bosque del Apache National Wildlife Refuge, New Mexico, are contained in a tab-delimited text file (camera_elk_counts.txt). This file contains 5 columns and 2,428 records. The ‘Camera’ column contains a unique identifier for each camera location. The ‘Date’ column contains the date of the image and it is formatted as year month day hour minute second. The ‘Bulls,’ ‘Cows,’ and ‘Calves’ columns contain counts of the respective age-sex classes for the image.

Found at DOI: <https://doi.org/10.3996/012018-JFWM-008.S2> (74 KB TXT).

Data S3. Two data input files for Program MARK (Mark_Resight_2012.inp and Mark_Resight_2013.inp) used to fit mixed logit-normal mark-resight models of adult elk *Cervus elaphus* abundance for January 2012 and 2013 at Bosque del Apache National Wildlife Refuge, New Mexico. These files are ASCII text files. For additional information regarding the format of data input files for Program MARK, consult <http://www.phidot.org/software/mark/>.

Found at DOI: <https://doi.org/10.3996/012018-JFWM-008.S3> (1 KB TXT).

Text S1. This supplement is a template population model to simulate the dynamics of the female segment of the elk *Cervus elaphus* herd at Bosque del Apache National Wildlife Refuge, New Mexico, using Program R (R Core Team 2013). We incorporated demographic stochasticity, temporal variability, and sampling variance for adult survival and juvenile recruitment into the iteration loop. We also included demographic stochasticity for the proportion of calves that were female. Estimates include both the proportion and number (given initial population sizes) of females to harvest to maintain a stable female population. This code is intended to provide a guide for incorporating uncertainty into simulations of ungulate population dynamics.

Found at DOI: <https://doi.org/10.3996/012018-JFWM-008.S4> (19 KB DOCX).

Reference S1. U.S. Fish and Wildlife Service. 2013. Emergency elk management: environmental assessment for Bosque del Apache National Wildlife Refuge. Albuquerque, New Mexico: U.S. Fish and Wildlife Service.

Found at DOI: <https://doi.org/10.3996/012018-JFWM-008.S5> (828 KB PDF).

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