

# Regulating overabundant ungulate populations: An example for elk in Rocky Mountain National Park, Colorado

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## Abstract

In many areas of the world, populations of native ungulates have become so abundant that they are believed to be harming vegetation and disrupting ecosystem function. Methods for controlling overabundance populations include culling animals from the population and controlling fertility using contraceptives. However, understanding the feasibility these alternatives requires insight into their long-term effects on populations.

We constructed a simulation model to evaluate options for regulating elk populations in and around Rocky Mountain National Park and used the model to compare different treatment options. Methods were evaluated with respect to the time required to reduce the population to a target level, the number of animals treated and/or culled and the risk of extinction. We contrasted culling with lifetime-effect contraceptives and yearlong contraceptives. Lifetime contraceptives required treating the fewest animals to maintain the population at desired targets. However, this approach also causes the greatest population variability and potential risk of extinction. Yearlong contraceptives required treatment of dramatically more animals but had essentially no extinction risk whereas culling produced intermediate levels of both extinction risk and number of animals treated. These results characterize the risks and benefits of alternative control strategies for overabundant wildlife. They emerge from a modeling approach that can be broadly useful in helping managers in choose between alternatives for regulating overabundant wildlife.

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**Keywords:** *Cervus elaphus*; Culling; Immunocontraception; Simulation modeling

## 1. Introduction

Overabundant populations of ungulates frequently exert enduring effects on the structure and composition of plant communities and often limit the abundance of other wildlife (Jewell and Holt, 1981; Diamond, 1992; Garrett et al., 1993). Ungulate browsing has been shown to influence vegetation composition (Horsley et al., 2003; Kraft et al., 2004; Rooney and Waller, 2003), regeneration (Liang and Seagle, 2002; Nomiya et al., 2003; Palmer et al., 2004) and reproduction (Brookshire et al., 2002). Although the impact of overabundant ungulates on vegetation is typically observed at relatively fine scales, the long-term consequences of this impact may be an important driver of

extensive change in vegetation composition (Pedersen and Wallis, 2004; Brown et al., 2001; Post et al., 1999; McLaren and Peterson, 1994). This impact of ungulates on vegetation can also influence the survival and abundance of birds (Berger et al., 2001), insects (Miyashita et al., 2004) and soil arthropods (Wardle et al., 2001). Overabundance of ungulates may also influence biogeochemical cycles. Recent evidence suggests that ungulates preferentially browse individual plants that are high in nitrogen (Tripler et al., 2002). Browsing appears to reduce soil nitrogen content, probably causing decreased nitrogen availability to plants and increasing microbial carbon:nitrogen ratios (Harrison and Bardgett, 2004). In addition, ungulates are thought to play a vital role in long-distance seed dispersal (Myers et al., 2004), a process that may be especially important as plant species move in response to changing climatic conditions (Vellend et al., 2003).

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These effects are particularly problematic in National Parks, because sport hunting is not allowed in many national parks of the continental US and because the parks are mandated to protect biological diversity, which may be harmed by excessive grazing and browsing (Porter et al., 1994; Frost et al., 1997; Wright, 1993, 1999; Porter and Underwood, 1999). In these areas, alternative techniques are essential for controlling ungulate population sizes.

Controlling fertility has been advocated as an alternative to lethal methods for regulating ungulate populations (Kirkpatrick and Turner, 1985; Garrott and Siniff, 1992; Garrott, 1995; Fayrer-Hosken et al., 1997; Muller et al., 1997; Nielsen et al., 1997). Fertility control methods employ contraceptive agents to render animals infertile, thus limiting population growth by limiting reproduction. If enough animals are treated, these methods can theoretically be used to reduce population sizes. Contraceptive treatments have been shown to be limit fertility in various mammals, including deer (Curtis et al., 2002), elephants (Delsink et al., 2002; Fayrer-Hosken et al., 2000), goats (Fayrer-Hosken et al., 2002), elk (Garrott et al., 1998; Heilmann et al., 1998), wild horses (Turner et al., 1997, 2001, 2002), burros (Turner et al., 1996), mice (Millar et al., 1989), and kangaroos (Nave et al., 2002).

Although fertility control techniques are widely advocated as a substitute to lethal control, few studies have attempted to quantify the feasibility of alternative contraceptive treatment strategies (Porter et al., 1994; Tuytens and Macdonald, 1998). Unanswered questions include: How do treatment rates change for contraceptives of different duration? How effective are fertility control methods for reducing a population and how long does the reduction require? Perhaps most important, what is the risk that the population will become extinct as a consequence of the fertility control agents? Addressing these questions with traditional manipulative or observational experiments is unfeasible because it would require extremely long time periods, expensive treatment schemes and potential risk of overpopulation or extinction for many of the populations examined.

Simulation models provide an excellent alternative approach to examining the consequences of various fertility control strategies (Nielsen et al., 1997; Starfield, 1997; Hobbs et al., 2000). Modeling exercises can examine the impacts of removing animals, treating animals with contraceptive agents, or a combination of these two approaches to population control. Once the effect of contraceptive agents on individual animals has been quantified, simulation models can provide insight into large-scale population-level response to treatment strategies, results that are not obtainable by traditional manipulative experiments or observational studies (Dell'omo and Palmery, 2002; Zhang, 2000). Models have been used to simulate the effect of contraceptive treatment on populations of horses (Gross, 2000), deer (Merrill et al., 2003), voles (Shi et al., 2002) feral cats (Courchamp and Cornell, 2000) and rodents (Chambers et al., 1997).

We developed a simulation model to evaluate alternative fertility control methods for well-studied elk *Cervus elaphus* population in Rocky Mountain National Park, near Estes Park, Colorado. There is widespread concern that populations of elk in National Parks in the western United States are causing harm to deciduous woody plant communities on low elevation winter ranges by preventing recruitment of young plants to mature stands. In response to this concern, Rocky Mountain National Park initiated a series of studies to examine impacts of the resident elk population on ecosystems of the Park. These studies offered evidence that communities of aspen and willow at low elevations are threatened by excessive browsing by wintering elk. The need to abate threats to these woody plant communities motivated the work we report here.

Our model was designed to simulate population-level response to alternative control strategies, including year-long and lifetime contraceptive treatments and/or harvesting options. Our overarching goal was to assess the magnitude of effort required to stabilize the population at target densities well below current levels and to quantify some of the risks involved in achieving those targets. Our specific objectives were to (1) estimate the number of animals that would need to be culled or treated with contraceptives during the next 30 years to reduce and maintain the elk population at pre-determined target sizes, (2) approximate the time required to reach the target population using alternative reduction methods, and (3) quantify the population variability around the target and the potential risk of extinction. This modeling study provides insight into the feasibility, risks and potential benefits of alternative population control strategies that would be difficult, expensive, and risky to obtain via experimental manipulation.

## 2. Methods

### 2.1. Modeling approach

Rocky Mountain National Park offers a particularly good case study for examining the effects of fertility control because long-term investment in population data permitted development of a well-parameterized, stage-structured model of population dynamics (Lubow et al., 2002). We combined this specific model with the general approach to modeling fertility control outlined in Hobbs et al. (2000). Thus, our model included three age classes (calves, yearlings, and adults) in three sex classes (male, fertile female, and infertile female) for a total of nine potential states (Fig. 1). Census in the model occurred at midwinter and we assumed that culling and fertility control treatments occurred immediately before census (Fig. 1). Our model examined the elk population on the east side of Rocky Mountain National Park and utilized values for initial population size and model parameters based on estimates generated by Lubow et al. (2002).

2.2. Scenarios

We examined the ability of population control techniques to reduce the total population size to a designated target and to maintain the population at the target (Table 1). We simulated 10 scenarios consisting of five different treatment options and two target population sizes (determined by management goals at Rocky Mountain National Park): 700 and 300 animals. Options for management were culling alone, culling used in combination with fertility control and fertility control alone. Two types of fertility control were represented in our simulations. The first type was chosen to mimic currently available technology that requires animals to

be treated with contraceptives annually to maintain infertility. We refer to these as yearlong contraceptives. The second type represented technology under development that requires that animals to be treated only once to cause lifetime infertility. We refer to these as lifetime contraceptives.

We divided each population control alternative into two phases, a reduction phase and a maintenance phase. During the reduction phase, culling or treatment rates were chosen to bring the population near the target and during the maintenance phase these rates were set to maintain the population at that target.

Our examination of each population control strategy included two types of analyses, deterministic and stochastic. Deterministic analyses assumed that treatment could be imposed perfectly and that population trends were not affected by annual variation in survival and recruitment. These runs were used to compare the efficacy of control options without considering variation stemming from weather fluctuations and random population processes. Stochastic analyses assumed that treatment could only be imposed based on imperfect knowledge of the population and that population trends were affected by annual variation in weather. Thus these stochastic runs include random variability and (using the “optimized” treatment and culling rates from the deterministic runs) provide insight into the expected actual range of outcomes for each scenario.

Strategies for Elk Population Control

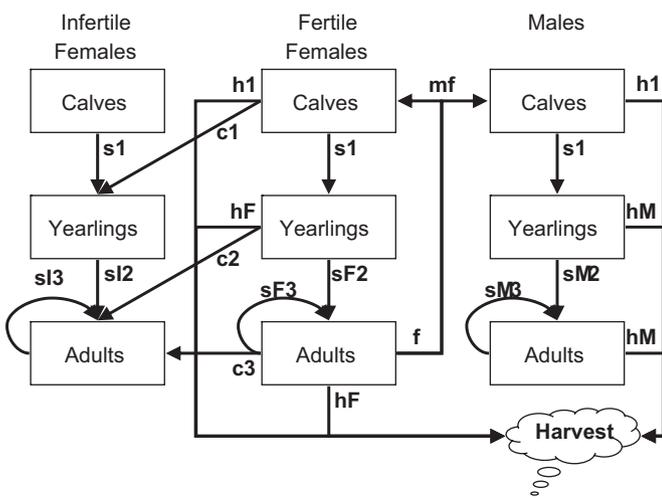


Fig. 1. Schematic of model structure used to simulate alternative population control strategies for overabundant elk in Rocky Mountain National Park. Parameters labels: *s* is survival rate, *c* is contraceptive treatment rate, *h* is harvest rate, *f* is fertility rate, *mf* is proportion of male and female calves, *f* is fertility rate; 1, 2, and 3 are rates for calves, yearlings and adults, respectively; *M*, *F*, and *I* are rates for males, fertile females and infertile females, respectively.

2.3. Deterministic model runs

In deterministic model runs we estimated the culling or treatment rates that minimized the number of animals treated subject to the following constraints:

- (1) The population must be within 20 animals of the target population size no later than 20 years after initiating treatment.

Table 1  
Model results for simulations of alternative strategies for Elk population control in Rocky Mountain National Park

Target population size	Reduction method	Reduction duration	Maintenance method	Total number of animals treated	Years required to reach the target	Mean years below target range	Mean years above target range	Probability of extinction
700	Culling	2	Culling	2011 (1392–2141)	2 (2–3)	2	5	0
700	Culling	10	Lifetime	716 (498–736)	7 (5–29)	4	4	0
700	Culling	10	Yearlong	2430 (1011–2571)	9 (4–29)	2	4	0
700	Lifetime	2	Lifetime	617 (484–628)	9 (3–29)	3	9	0
700	Yearlong	10	Yearlong	6003 (4807–6227)	8 (4–29)	1	3	0
300	Culling	7	Culling	2947 (2179–3969)	7 (7–29)	1	5	0
300	Culling	3	Lifetime	954 (741–963)	9 (5–29)	3	9	0.099
300	Culling	8	Yearlong	2964 (1469–3057)	8 (15–29)	1	8	0
300	Lifetime	2	Lifetime	668 (581–669)	22 (6–29)	3	17	0.223
300	Yearlong	14	Yearlong	6550 (6283–7357)	14 (14–15)	0	1	0

Ten scenarios were defined by two alternative target population sizes (700 and 300) and five combinations of population control methods for the reduction and maintenance phases. Results include the total number of animals treated (95% confidence intervals derived from simulations with stochastic variability), the years required to reach the target population size (95% confidence intervals), the average years below and above the target range during the maintenance phase (from stochastic runs), and the probability of extinction (from stochastic runs).

- (2) The population must be within 20 animals of the target population size after 30 years.
- (3) The reduction phase can last for no more than 10 years, except for the scenarios that examine yearlong contraceptives in the reduction phase. These scenarios were allowed up to 15 years for the reduction phase because yearlong contraceptives were not capable of reaching all targets within 10 years under the constraints of constant treatment number during reduction and not attempting to treat more animals than are available. A scenario with yearlong contraceptives requires very high treatment levels to utilize only a 10-year reduction phase and by the end of that phase the number of animals treated would be greater than the number of females in the population.
- (4) To reduce risk of extinction, the number of fertile females in a population treated with contraceptives could not drop below 15% of the target population size.

For each of the management options, we estimated the total number of animals that needed to be culled or treated during the 30-year simulation and the time required to reach the target for each scenario. In scenarios involving lifetime contraceptives, we assumed that animals were marked such that their fertility status was known and animals that were infertile were not treated more than once.

#### 2.4. Stochastic model runs

In stochastic model runs, we used the treatment or culling rates determined in the deterministic model runs and included variability due to weather conditions, random population variation not represented by the model, and management responses to censuses of the population. Weather values (winter temperature, summer temperature and summer precipitation where needed) for each future year were randomly chosen from normal distributions with means and standard deviations based on historic data (see Lubow et al., 2002). We also added random variation in population numbers due to process error not represented by effects of weather. This error might include emigration or immigration or random fluctuations in vital rates. We implemented this variation in the model by choosing a random variate from a normal distribution with mean = 0 and standard deviation = 0.1 for each year of the simulation. We then multiplied this variate by the model's estimate of the number of fertile yearling and adult females and added the product to the model estimate.

In addition, the stochastic runs explicitly simulated the consequences of managers modifying culling or treatment rates during the scenario in response to observed population fluctuations. It is reasonable to expect that managers will alter treatment based on data acquired during a 30-year management plan, rather than blindly follow the treatment and culling rates prescribed by the model. We

represented this adaptive management response by ceasing treatment or culling when the population dropped below a threshold and elevating treatment by 10% during each year that the population exceeded a threshold. Lower and upper thresholds were defined as the 10th and 90th percentiles of a normal distribution centered at the target with standard deviation equal to the standard deviation of census estimates observed in the field. This process minimized the frequency of falsely predicting a departure from the target and could be easily adopted by managers in the future.

Culling can reduce a population to a target within a single year, but populations regulated by fertility control cannot decline more rapidly than the natural adult mortality rate. Thus, lifetime contraceptives can produce a situation in which the population is declining, but remains above the target. Continuing to increase treatment in this situation can easily result in loss of fertility in all of the fertile females, causing the population to have zero fecundity and eventually becoming extinct. To eliminate the possibility of initiating adaptive management prior to population reduction and thereby excessively reducing the population, the adaptive management approach outlined above was initiated in each iteration only after the population had dropped to within a 90% C.I. around the target as defined by the standard error of census observations.

To generate predictions that included stochastic processes, we included weather variation, population variation and adaptive management responses to data, ran each scenario for 1000 iterations and recorded the outcome of each iteration. These results were used to estimate the number of years the population would be outside of an acceptable range, defined as the target + 100 animals (consistent with management objectives at Rocky Mountain National Park). We also used the 1000 iterations to generate a probability of local extinction and to calculate 95% confidence intervals on the number of animals treated and the time required to reach the target. Because culling can reduce the population immediately, we only examined the time required to reach the target for scenarios that used fertility control in the reduction phase.

### 3. Results

#### 3.1. Number of animals treated

We observed similar relative patterns in the number of animals treated in for both population sizes. Fertility control using lifetime contraceptives in the reduction and maintenance phase was more efficient than any of the other control techniques (Table 1). Culling in the reduction phase combined with lifetime fertility control in the maintenance phase displayed the next lowest treatment rates and using culling in both phases required intermediate treatment levels. Culling in the reduction phase followed by yearlong contraceptives in the maintenance phase required slightly

higher treatment rates whereas using yearlong contraceptives for both phases required the highest treatment rates.

### 3.2. Time required to reach target population

Scenarios utilizing culling for reduction can reach the target population immediately. Although fertility control can be more efficient than culling in terms of the number of animals treated, the time required to bring a population to the target density is always higher for fertility control than for culling because the population cannot decline faster than the natural mortality rate (Table 1). For both target population sizes the shortest time to the target was observed in the scenarios with yearlong fertility control in both phases and using lifetime contraceptives required more time, especially for the low target population size.

### 3.3. Population variability and extinction risk

**700 Animal Target:** Variability of the population around the target was greatest in the scenario with lifetime contraceptive in both phases, which showed an average of 3 years with fewer than 100 animals below the target and 9 years with more than 100 animals above the target (Table 1). Using culling for reduction and lifetime contraceptives for maintenance had the next highest variability, with an average of 4 years above and below the target range. Culling for reduction and maintenance produced 2 years below the range and 5 years above the range. The least variability was observed in the scenario with yearlong contraceptives in both phases, which had only 1 year below and 3 years above the target. Substituting culling for the reduction phase increased the average variability to 2 years below and 4 years above the target range. None of the scenarios examining the 700 animal target indicated any risk of extinction.

**300 Animal Target:** The strategy with yearlong contraceptives in both phases displayed the least variability, with an average of 0 and 1 year below and above the target range, respectively. Substituting culling in the reduction increased the variability to 1 year below and 8 years above the target range. The greatest variability for these scenarios was an average of 3 years below and 17 years above, exhibited by the strategy utilizing lifetime contraceptives in both phases. Using culling followed by lifetime contraceptives was the next most variable, with 3 and 9 years below and above the range. Culling for reduction and maintenance had intermediate variability, averaging 1 year below the range and 5 years above. We observed extinction in some iterations of scenarios involving lifetime effect fertility control agents. Culling in the reduction phase followed by lifetime contraceptives had an extinction probability of 0.099, while using lifetime contraceptives in both phases produced an extinction probability of 0.223. The other three scenarios showed no risk of extinction.

## 4. Discussion

### 4.1. Number of animals treated

Our modeling suggest that lifetime duration contraception is more efficient than culling when efficiency is measured in terms of the total number of animals that must be treated to maintain a population at a given target. This result occurs because of density-dependent feedback to population growth rates. Density dependence occurs whenever the number of animals surviving to reproductive age per reproductive female decreases with increasing population size and has been modeled in numerous previous studies of contraceptive population control (i.e. Courchamp and Cornell, 2000; Shi et al., 2002; Hobbs et al., 2000; Zhang, 2000). In our model, density dependence decreases per capita recruitment as population size increases. Immediate population decline due to culling minimizes the effect of population density on recruitment, allowing more animals to be born per female than would have been born if culling had not occurred. Controlling animals with contraceptives does not produce a rapid reduction in population size, and as a result, maintains the negative effect on per-capita recruitment rates. Because observational data suggest that calf survival and recruitment depended on population size (Lubow et al., 2002) and this density dependence is incorporated in our models, it is not surprising that lifetime contraceptives required lower treatment rates than were required by culling to achieve the same target densities. Some previous population modeling studies have found that density dependence can cause contraceptives to be more efficient than culling for various species including (i.e. Shi et al., 2002; Porter et al., 2004; Hobbs et al., 2000). However, other results suggest that in some cases density-dependent effects may not be sufficient to outweigh the limited efficacy of contraceptives compared to culling (i.e. Hone, 1992; Barlow et al., 1997; Nielsen et al., 1997). In addition, density-dependent effects may depend heavily on the relationship between population size and carrying capacity (Porter et al., 2004) or the intensity of contraceptive treatment, with intermediate levels of contraception potentially increasing population growth (Twigg et al., 2000; Caughley et al., 1992). Thus, our result that contraceptive treatment are more efficient than culling may be specific to the intense treatment of overpopulated elk that we simulated.

There is another important caveat in our conclusions about the relative efficiency of lifetime contraceptives. We assumed that all animals were marked and, as a result, that animals that had been treated with contraceptives were never treated again. If this assumption is not valid, then far more doses of contraceptives would have to be delivered to achieve the same level of infertility in the population (Hobbs et al., 2000). However, using long-duration contraceptives, it might be possible to annually treat a sufficient number of calves (all of which are known to be potentially fertile) to maintain animals at the target using only

temporary marks. Temporary marking of treated calves could prevent animals from being handled more than once. The absence of marks on adult animals would make it far more difficult to assess the fertility status of the population, and hence would increase the risk of accidentally treating all females and causing extinction.

4.2. Time required to reach the target population size

Using culling to reduce an overabundant population allows complete control over the amount of time required to reduce the population to the target level. Only 1 year is needed in the model to reduce an overabundant population to any hypothetical, less abundant target using culling. The differences in reduction times (Table 1 and Fig. 2) observed in our simulations with culling in the reduction phase are a result of our primary objective of minimizing the number of animals to be treated. We allowed the duration of the reduction phase to vary along with the number of animals treated in each class in order to determine the combination of treatment regime and reduction duration that achieved the management objectives by treating the minimum number of animals.

We observed that less time is required to reach the target population when reduction is accomplished by yearlong contraceptives compared to lifetime contraceptives. Note that this is the time required to reach the target, not the duration of the reduction phase, which was allowed to be longer for yearlong agents and may partially account for the difference in time to reach the target between yearlong and lifetime contraceptives. We observed high variability in the time required to reach the target for all contraceptive scenarios except the one using yearlong contraceptives to reach the low target. This scenario was unique because it treated essentially all fertile females every year until reaching the target, meaning that population dynamics during that time were driven strictly by adult survival, which is a process not influenced by stochastic variability in this model. Other scenarios had at least some recruitment and thus calf survival, both processes influenced by stochastic variability, creating higher variation in population size through time and higher variation in the time required to reach the target population size.

The stochastic processes incorporated into our simulations may have minimized the difference in reduction duration observed between the lifetime and yearlong contraceptives.

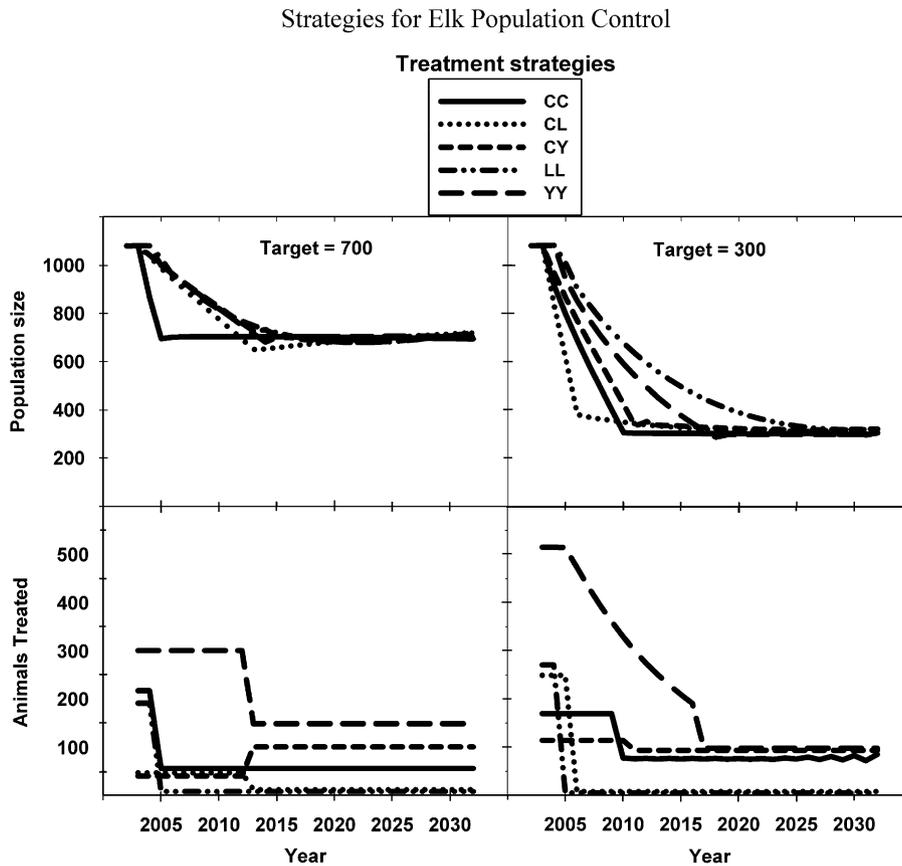


Fig. 2. Population size (top two panels) and animals treated (bottom two panels) vs. year for five different population control strategies and two target population sizes (left versus right panels) for an overabundant elk population (initially 1100 animals) in Rocky Mountain National Park. Abbreviations for population control strategies are: CC = culling for reduction and maintenance; CL = culling for reduction and lifetime contraceptives for maintenance; CY = culling for reduction and yearlong contraceptives for maintenance; LL = lifetime contraceptives for reduction and maintenance; YY = yearlong contraceptives for reduction and maintenance.

The high values on the upper end of the 95% C.I.s for the time required to reach the target may be a result of initiating adaptive management only after the population was reduced to near the target. If stochastic processes maintained the population at very high levels through the reduction phase, adaptive management would not be initiated, but treatment rates would drop to the level dictated by the maintenance phase. In these cases, the population remains at high levels and treatment is not intensified by adaptive management because of the restrictions placed on adaptive management during the reduction phase.

4.3. Variability around the target

The treatment strategy that produced the least variability around the target used yearlong contraceptives in both the reduction and maintenance phases. For both target population sizes, this strategy was least variable, followed by the strategy that used culling for reduction, followed by yearlong contraceptives in the maintenance phase. Controlling populations with yearlong contraceptives is likely the least variable because these populations are able to respond quickly to altered treatment rates during adaptive management. Because effects of yearlong contraceptives expire at the end of each year, ceasing treatment causes an immediate and dramatic increase in the overall fertility of the population. Gross (2000) observed similar low levels of variability in wild horse populations treated with short-duration contraceptives compared to culling.

Responses of populations controlled by culling and lifetime contraceptives, on the other hand, involve time lags—when adults are culled, it takes time for them to be replaced by offspring that must grow to reproductive age. Similarly, when animals are treated with lifetime effect contraceptives, ceasing treatment does not increase the population growth rate immediately. Instead, the growth rate does not increase until fertile animals accumulate in the population, and this accumulation occurs slowly because there are relatively few animals producing offspring. Because treatment with lifetime contraceptives had the greatest time lags in population response to cessation of treatment in adaptive management, these strategies also had the highest levels of variability around the target. The high variability observed in scenarios with lifetime contraceptives may also be a consequence of the short reduction phase with high treatment rates. Treating a high proportion of the population with lifetime contraceptives leaves very few remaining fertile females, whose viability is more susceptible to random demographic and environmental fluctuations that a large population, especially since population growth is strongly limited by population density.

4.4. Extinction risk

We observed substantial risk of extinction only in options that used lifetime contraceptives to maintain the

population at the 300 animal target population size. Populations treated with lifetime contraceptives are most susceptible to extinction because the number of fertile females is very low during the reduction period, and hence are exposed to all of the demographic risks associated with small population size. As a result, even modest mortality caused by stochastic processes can cause the fertile female portion of the population to decline to levels insufficient to offset natural mortality. Our strategies that used lifetime contraceptives for reduction all found that a 2-year reduction period was most efficient (Table 1). The absence of extinction risk in all other scenarios suggests that the relatively modest adaptive management regime applied in our models is effectively counteracting the stochastic variability introduced by weather and random population fluctuations. The approach of completely eliminating treatment whenever the population is determined to be low is a rapid and strong response to excessive declines in population size, and may be partly responsible for the observed long-term population stability using all options except lifetime fertility control.

5. Conclusions

Our studies revealed strengths and liabilities in all options for regulating the elk population in Rocky Mountain National Park. Although our simulations do not include the possible effects of migration to or from this population, a process that is likely to be important in

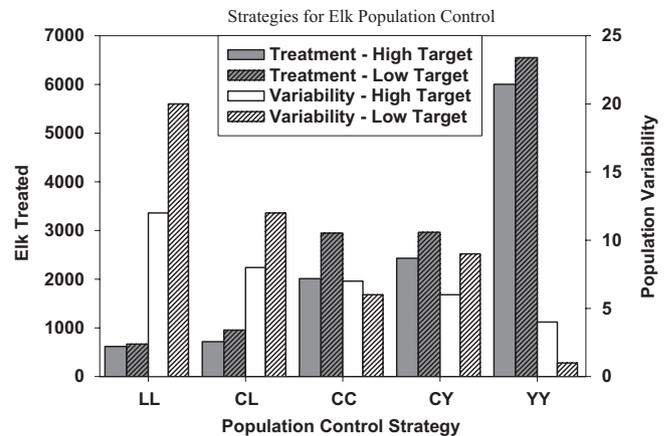


Fig. 3. Summary of results for simulations of population control for an overabundant elk population (initially 1100 animals) in Rocky Mountain National Park. Gray bars are the total number of animals treated (dosed with contraceptives or culled) for reduction and maintenance phases totaling 30 years. White bars are the number of years during the maintenance phase that the population deviated more than 100 animals from the target size and are a general indicator of extinction risk. Crosshatched bars of either gray or white relate to scenarios with a low population target (300 animals) whereas open bars relate to scenarios with a high population target (700 animals). Abbreviations for population control strategies are: LL = lifetime contraceptives for reduction and maintenance; CL = culling for reduction and lifetime contraceptives for maintenance; CC = culling for reduction and maintenance; CY = culling for reduction and yearlong contraceptives for maintenance; YY = yearlong contraceptives for reduction and maintenance.

dictating population dynamics (Merrill et al., 2003), these results provide insight into the costs and benefits of alternative control strategies for overabundant wildlife populations in general (Fig. 3). Lifetime duration contraceptives require treatment of the fewest animals to achieve target population sizes. However, this option entails high levels of variation around the target and, when the target population is very small, a very high probability of local extinction even when adaptive management is used in an attempt to minimize that risk. In contrast, utilizing yearlong contraceptives produces virtually no risk of extinction, but requires treating dramatically more animals to achieve and maintain target population size. Culling was intermediate to the two fertility control options. It was reasonably efficient in terms of number of animals treated to stabilize the population at the target and allowed for reasonable stability around the target. Our results suggest that although small target population size is attainable, low targets require higher treatment rates, take longer to reach the target population for reduction periods that use contraceptives and include higher variability and extinction risk.

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