Effects of Bull Age on Conception Dates and Pregnancy Rates of Cow Elk
Author(s): James H. Noyes, Bruce K. Johnson, Larry D. Bryant, Scott L. Findholt, Jack Ward Thomas
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EFFECTS OF BULL AGE ON CONCEPTION DATES AND PREGNANCY RATES OF COW ELK

JAMES H. NOYES, Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA
BRUCE K. JOHNSON, Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA
LARRY D. BRYANT, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA
SCOTT L. FINDHOLT, Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA
JACK WARD THOMAS, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA

Abstract: Productivity of cows in many Rocky Mountain elk (Cervus elaphus nelsoni) populations of northeast Oregon has declined over the last 30 years. Numbers of mature bulls declined concurrently, suggesting a potential link that accounts for declining productivity. We evaluated the influence of bull age on conception dates and pregnancy rates of cow elk within a 78-km² enclosure on the Starkey Experimental Forest and Range in northeast Oregon from 1989 to 1993. We allowed a single cohort of bulls to mature from 1 1/2 to 5 1/2 years and function as principal herd sires. Subsequent male offspring were reduced in numbers through hunting and trapping. We estimated conception dates, pregnancy rates, body condition, age, and lactation status of cows killed in December. Conception dates occurred earlier as bull age increased (P = 0.0001) and were significantly different between bulls ≤2 years and ≥3 years of age. The rut became more synchronous and shortened from 71 days (n = 26) when breeding was by yearling bulls to 41 days (n = 33) when 5-year-old bulls were the principal sires. Pregnancy rates increased from 89 to 97% as bull age increased, but not significantly (P = 0.62). Cow body condition was highest (P = 0.004) in 1989 when breeding was by yearling bulls. To enhance herd productivity we recommend that elk hunting seasons be designed so that older bulls (≥3 yr) are retained in the population.

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Key words: breeding, bull age, Cervus elaphus, conception date, condition, elk, fetal age, hunting, kidney fat, Oregon, pregnancy rate, reproduction.

Winter calf:cow ratios for elk have declined from >50:100 in the early 1960s to <35:100 in 1989 and 1990 in northeast Oregon (Schommer 1991). During this same period, post hunting season bull:cow ratios declined from >15:100 to <5:100 in many management units (Schommer 1991) presumably because of increased hunting pressure, loss of hiding cover, and increases in road access (Leckenby et al. 1991). Because bull escapement declined (Leckenby et al. 1991) with few mature bulls surviving hunting seasons, we hypothesized that declines in productivity were caused, in part, by yearling bulls serving as principal herd sires.

Mature bulls ordinarily function as principal sires of polygamous harems, often resulting in high pregnancy rates and early and synchronous breeding and parturition (Bubenik 1982). Breeding behavior (Prothero et al. 1979, Squibb 1985) and fertility (Lincoln 1971) differ be-

1 Present address: USDA Forest Service, P. O. Box 96090, 4 N.W., Washington, D.C. 20090, USA.

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tween yearling and older bull elk. Conception dates were delayed when breeding was by mostly yearling bulls compared to older bulls (Follis 1972, Hines and Lemos 1979), but Follis (1972) was unable to detect changes in pregnancy rates with different ages of bulls.

Cow body condition and age during breeding also influence the timing and success of conception (Trainer 1971, Mitchell and Lincoln 1973, Hines et al. 1985, Albon et al. 1986). To our knowledge, however, no study varied bull age while concurrently measuring or controlling most other aspects of elk reproduction.

Our purpose was to evaluate effects of bull age on elk reproduction in a closed but free-ranging elk population. Our objectives were to compare conception dates and pregnancy rates of cow elk bred by bulls of different ages, and to examine the influence of cow age, cow condition, and lactation status on these reproductive parameters.

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J. Nothwang, C. Poppenwimer, R. Stussy, B. Swearingen, T. Westfall, and volunteers who assisted with this study. C. E. Trainer provided guidance in laboratory exams of elk reproductive organs. N. Golly and R. Green assisted with uterine and kidney measurements. L. L. McDonald, W. P. Erickson, and D. Marx provided statistical assistance. D. A. Leckenby and L. J. Erickson were instrumental in initiating the study. J. Cook, T. O’Neill, R. Stussy, and C. E. Trainer reviewed the manuscript. The study was supported by Federal Aid in Wildlife Restoration, the Oregon Department of Fish and Wildlife, and the USDA Forest Service. Big game research at Starkey is in accordance with approved animal welfare protocol (Wisdom et al. 1993).

STUDY AREA

We conducted the study during 1989–93 at the USDA Forest Service Starkey Experimental Forest and Range (Starkey), located 35 km southwest of La Grande in northeast Oregon. Elevation ranged from 1,116 to 1,502 m. Vegetation was a mosaic of forest stands and open areas. Forest vegetation was dominated by ponderosa pine (Pinus ponderosa) at lower elevations, and lodgepole pine (P. contorta), grand fir (Abies grandis) and Douglas fir (Pseudotsuga menziesii) on north aspects and higher elevations. Grassland vegetation composition was variable and typically dominated by bluebunch wheatgrass (Agropyron spicatum) and Idaho fescue (Festuca idahoensis). The soils and plant communities within the study area have been described by Strickler (1965). Annual precipitation averaged 51 cm, most (2/3) in the form of snow from November through March (Strickler 1965). Rains in April, May, and June made up most of the remaining precipitation. Average mean temperatures were 18 C in July and -4 C in January.

Starkey was traditional spring, summer, and fall range with elk use in winter limited to periods when snow depths were at a minimum (Skovlin et al. 1968). Starkey was enclosed in fall 1987 by a game-proof fence 2.6 m tall that eliminated immigration and emigration of elk within the 78-km² study area. Starkey was open to the public from about mid-April to mid-December, and public entry was limited to 1 access point. Open road density was 0.6 km/km². Public use consisted primarily of mushroom picking and wildlife viewing. Controlled deer hunts with low densities of hunters (0.3–0.9/km²) were conducted within the study area. Firewood cutting was not allowed. Starkey was subdivided with cattle fences into 3 main pastures, which were grazed by 500 cow/calf pairs in a deferred rotation grazing system from mid-June to mid-October. Logging activities were restricted to timber sales of 4,900 m³ (2.1 million board feet [mmbf]) during summer and fall 1989 and 700 m³ (0.3 mmbf) during summer 1993. Further descriptions of Starkey were provided by Johnson et al. (1991) and Skovlin (1991).

METHODS

Herd Management

The study population of elk was established when we enclosed the resident population within the fence in 1987. In winter 1988–89, we trapped 288 cows, 185 calves, and 39 bulls and fed them on a feed ground, where we marked animals and obtained age, sex, weight, and blood data (Wisdom et al. 1993). During helicopter surveys in March 1989, we observed 34 cows, 13 calves, and 4 bulls still in the study area. In spring 1989, we released 208 cows, 51 bull calves, and 55 female calves into our study area. Ninety-seven cows were marked with neck collars, and all but 7 cows and 6 calves were marked with eartags.

We attempted to remove all antlered elk from this population starting in fall 1988 when 104 bulls were killed during controlled hunting seasons. All bulls trapped on the feed ground were removed from the study area. Using darting and gunning from a helicopter, we removed 14 bulls ≥2 years old in June and early September 1989. Finally, we removed 2 adult bulls in early October 1989, and estimated that 2 adult bulls remained in the population.

The minimum estimated cow population was 242 in spring 1989, but we knew we did not count all the elk within Starkey during the helicopter survey. We used mark-recapture of cows marked in winter and killed during the cow hunt in December 1989 to estimate the cow population (±95% CI) to be 264 ± 55 adult cows (≥2 yr old) or 361 ± 82 cows ≥ yearlings. We then developed a Pop-II model (Barthlow 1990) of the population in spring 1991, using observed sex and age ratios from helicopter surveys in winter 1990–91, numbers of yearling bulls killed in August 1990, and numbers of
animals trapped on the feed ground. The model was aligned annually on end-of-fall and end-of-winter calf:cow ratios obtained during helicopter surveys or from animals trapped on the feed ground. From this model, we estimated 397 cows (78 yearlings and 319 ≥2 yr old), 76 yearling bulls, and 4 adult bulls comprised our population at the start of the rut in 1989 (Table 1). Two of the 4 adult bulls were killed in early October 1989 by project personnel.

We then constructed an empirical spreadsheet model in Lotus 1-2-3 that mimicked our Pop-II model. We modified the mortality tables in our spreadsheet model to enter age- and sex-specific mortality events at specific times of the year (B. K. Johnson, Oreg. Dep. Fish and Wildl., unpubl. data).

We validated our model using mark-recapture of collared elk during winters 1991–92 and 1992–93. All model estimates for cow population size fall within the 95% confidence intervals of all data sets used to validate the model (B. K. Johnson, Oreg. Dep. Fish and Wildl., unpubl. data). In fall 1994, winter 1994–95, and fall 1995, we attempted to remove all antlered elk from the population using 5 controlled hunts, trapping, and helicopter darting. Before any hunts, we estimated 34, 13, 4, 3, 4, 46, and 1 bulls from yearling to 7 years of age, respectively, occurred in the population. We removed 31, 14, 4, 2, 5, 47, and 1 bulls aged 1 to 7, leaving an estimated 1 bull in our population. We are confident our estimate of the cow population is both reasonably precise and accurate, but we are unable to place a confidence interval around our model estimate.

We maintained the bull:cow ratio of the study cohort between 18:100 and 20:100 during the 5 years of our study (Table 1). We used this bull:cow ratio to minimize confounding effects of numbers of bulls. This cohort of bulls was allowed to mature from 1 1/2 to 5 1/2 years and function as principal herd sires. From 1990 to 1993, we held hunts for spike bull elk in mid-August to reduce the number of yearling bulls in the population before the breeding season. Males trapped in winter younger than the study cohort were released outside Starkey.

During normal or severe winters, a significant proportion of the elk moved to the winter feed ground and were fed supplemental forage (Table 1). Elk were fed 3.5–4.5 kg/elk/day of alfalfa pellets or hay. Our objective was to reduce the effects of variable winter severity on elk reproduction.

**Reproductive Data**

We collected reproductive tracts (uterus and ovaries), udders, lower incisors, and kidneys from cow elk killed by hunters during the first 2 weeks of December. Hunters were required to view an instructional video on collecting these parts before hunting. We designed the hunts to provide >25 fetuses from adult cows (≥2 yr old), in order to meet our objective of a minimum precision of ±7 days in mean conception dates at 90% confidence.

We calculated conception dates by subtracting estimated ages of macroscopic embryos (Morrison et al. 1959) from known dates of harvest. Conception dates were coded as the number of days past 20 August, and were advanced by 1 day for the leap year which occurred in 1992. For embryos ≤64 mm, we measured the crown-rump length of the embryo while it was suspended in water; embryos >64 mm in length were measured with a forehead-rump length (Trainer 1971). To reduce observer bias, the

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Table 1. Estimated number of yearling and adult elk present during the rut at the Starkey Experimental Forest and Range, Oregon, 1989–93.

<table>
<thead>
<tr>
<th>Year</th>
<th>Cows</th>
<th>% Fed&lt;sup&gt;a&lt;/sup&gt;</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Total bull ratio&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Study bull ratio&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>397</td>
<td>66</td>
<td>76&lt;sup&gt;d&lt;/sup&gt;</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td>20</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td>412</td>
<td>13</td>
<td>21</td>
<td>74&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2</td>
<td></td>
<td></td>
<td>24</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td>395</td>
<td>45</td>
<td>24</td>
<td>6</td>
<td>72&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2</td>
<td></td>
<td>26</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td>346</td>
<td>3</td>
<td>17</td>
<td>17</td>
<td>70&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2</td>
<td></td>
<td>32</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>311</td>
<td>72</td>
<td>32</td>
<td>4</td>
<td>6</td>
<td>4</td>
<td>58&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2</td>
<td>34</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Proportion of cow population supplementedly fed the previous winter.

<sup>b</sup> No. bulls/100 cows.

<sup>c</sup> No. study cohort bulls/100 cows.

<sup>d</sup> Study cohort.
same person conducted measurements of the embryos during all 5 years of the study. Estimated ages of embryos were \( \geq 23 \) days \( (\bar{x} = 72) \), with the exception of 1 embryo estimated by extrapolation to be 18 days. The range of estimated ages \((18-103)\), was less than the gestation midpoint of 123 days \( \text{(Morrison et al. 1959)} \), beyond which most of the fetal growth occurs \( \text{(Robbins 1993)} \). Assessment of pregnancy and lactation status followed techniques by Trainer \( \text{(1971)} \). We tested blood samples for brucellosis \( \text{(Brucella abortus)} \) and leptospirosis \( \text{(Leptospira spp.)} \) to identify diseases that may influence elk reproduction. We based cow condition estimates on a modified kidney fat index \( \text{(KFI)} \) described by Trainer \( \text{(1971)} \). Ages of adult cows were determined by Matson's Lab \( \text{(Milltown, Mont.)} \) using cementum annuli counts \( \text{(Keiss 1969)} \) and from tagging records. We separated cows in 4 age classes \((1, 2, 3-13, \text{and} > 13 \text{yr old})\) to assess age-related effects on reproductive parameters. Flook \( \text{(1970)} \) observed a significantly lower pregnancy rate in cow elk \( \geq 13 \text{ years old} \).

### Statistical Analysis

We used a reciprocal transformation on dates of conception and a square root transformation on cow condition \( \text{(KFI)} \) to improve normality. We used \( P = 0.05 \) as the level of statistical significance for all tests.

**Conception Date.**—We compared conception dates among years using 1-way analysis of variance \( \text{(ANOVA)} \) and the LSMEANS method of multiple comparisons \( \text{(PROC GLM, SAS Inst. Inc. 1987)} \). We performed a Bartlett's test to assess equality of variances of transformed conception dates and could not reject the hypothesis of homoscedasticity. We made the assumption that although we measured year effects on conception dates as a result of the study design \( \text{(i.e., the same bulls were used during the 5 yr)} \), bull age accounted for the majority of those effects and did, in fact, represent the treatment.

We used stepwise multiple regression \( \text{(PROC STEPWISE, SAS Inst. Inc. 1987)} \) to assess the significance of bull age, KFI, cow age class, and lactation status in predicting conception date, and to compute the contribution of each variable \( (r^2) \) to the variation in conception date. We used \( t \)-tests \( \text{(PROC TTEST, SAS Inst. Inc. 1987)} \) to compare conception dates between lactating and nonlactating cows \( \geq 3 \text{ years old} \), because of bias in the proportion of 2-year-old cows that were lactating. Correlation analyses \( \text{(PROC CORR, SAS Inst. Inc. 1987)} \) were used to examine interactions among conception dates and KFI for lactating and nonlactating cows.

**Pregnancy Rate.**—We restricted our analysis of pregnancy to cows \( 2-13 \text{ years old} \) because of the potential lower productivity of yearling cows and cows \( > 13 \text{ years} \) \( \text{(Flook 1970)} \). We tested for differences in pregnancy rates among years with analysis of variance \( \text{(PROC CATMOD, SAS Inst. Inc. 1987)} \).

Logistic regression \( \text{(PROC LOGISTIC, SAS Inst. Inc. 1987)} \) was used to examine relationships between pregnancy and bull age and KFI, to determine whether we could predict the probability of a cow being pregnant. We used correlation analyses to evaluate interactions among pregnancy status, lactation status, KFI, and cow age class.

**Cow Condition.**—We used 1-way ANOVA \( \text{(PROC GLM, SAS Inst. Inc. 1987)} \) to compare KFI among years for all cows \( \geq 2 \text{ years old} \). We determined where differences occurred with the least squares means \( \text{(LSMEANS)} \) method of multiple comparisons. We used \( t \)-tests to compare KFI between lactating and nonlactating cows \( \geq 3 \text{ years old} \).

### RESULTS

**Conception Date**

Date of conception differed among years \( (F = 12.47; 4, 135 \text{ df} ; P = 0.0001) \), and bulls \( \geq 3 \text{ years old} \) of age bred earlier than bulls \( \leq 2 \text{ years of age} \) \( \text{(Table 2)} \). The largest differences in mean conception dates were between 5-year-old bulls \( \text{(21 Sep)} \) and yearling \( \text{(7 Oct)} \) or 2-year-old bulls \( \text{(3 Oct)} \). Cows bred by 3- or 4-year-old bulls had similar conception dates \( (P = 0.54) \), as did cows bred by yearling or 2-year-old bulls \( (P = 0.44) \) \( \text{(Table 2)} \). Cows bred by 5-year-old bulls conceived earlier than did cows bred during any other year \( (P \leq 0.02) \).

Conception dates were significantly related to bull age \( (P = 0.0001) \), cow lactation status \( (P = 0.0001) \), cow age class \( (P = 0.001) \), and KFI \( (P = 0.01) \). The regression model with these 4 independent variables accounted for 46% of the variation in conception date. The partial \( r^2 \) values associated with each variable were bull age \( (26\%) \), lactation status \( (12\%) \), KFI \( (3\%) \), and cow age class \( (5\%) \). Bull age and cow lactation status accounted for 83% of the variation in conception date explained by the regression model.
Mean conception date of nonlactating cows was significantly earlier (\( \bar{x} = 9 \) days) than for lactating cows in 3 of the 5 years (\( P \leq 0.02 \)). Conception date and KFI, however, were not directly correlated for either lactating (\( r^2 = 0.006; P = 0.509 \)) or nonlactating (\( r^2 = 0.007; P = 0.651 \)) cows.

The rut became more condensed as bull age increased, ranging from 71 days when yearling bulls were the primary sires to 41 days when 5-year-old bulls were the sires (Table 2). In 1993, with 5-year-old bulls as the sires, 52% of all conceptions occurred within the 1-week period from 15–21 September (Fig. 1). The cumulative percent of conceptions showed a shift toward earlier dates as bulls increased in age (Fig. 2). The 90th percentile pregnant cow was bred on 28 September by 5-year-old bulls and 21 October by yearling bulls (Table 2).

**Pregnancy Rate**

Pregnancy rates increased from 89% with yearling bulls as primary herd sires to 97% when 4- and 5-year-old bulls bred (Table 3), but the differences were not significant (\( P = 0.62 \)). Pregnancy was not related to either KFI (\( P = 0.167 \)) or bull age (\( P = 0.163 \)). Pregnancy rates were not correlated with KFI (\( r^2 = 0.011; P = 0.206 \)), cow age class (\( r^2 = 0.003; P = 0.537 \)), or lactation status (\( r^2 = 0.023; P = 0.071 \)). Results of blood testing revealed no diseases that may have affected pregnancy rates.

**Cow Condition**

KFI of cows ≥ 2 years old differed among years (\( F = 3.97; 4, 140 \) df; \( P = 0.004 \)), with 1989 significantly higher than all other years except 1991 (\( P = 0.06 \), Table 4). Nonlactating cows had significantly higher KFI (\( P < 0.0001 \)) than lactating cows.

**DISCUSSION**

Results of our study suggest that bull age significantly influenced timing and synchrony of the rut. The influence of bull age became apparent when bulls were 3 years old and increased as bulls aged to 5 years. These results support previous observations of earlier breeding by older bulls (Follis 1972, Hines and Lemos 1979). Ideally, our study should have been replicated, but it was both logistically and financially not feasible to replicate the facilities at Starkey.

Dates of conception may be influenced by cow condition (Trainer 1971, Mitchell and Lincoln 1973). Trainer (1971) reported that conception dates for lactating Roosevelt cow elk (C. e. roosevelti) were later than those for nonlactating cows, which he attributed to differences in physical condition. Likewise, at Starkey, nonlactating cows were in better condition (Table 4) and bred earlier than lactating cows. We do not have evidence, however, that cow condition (as exhibited by either lactation status or KFI), affected the timing of conception to the degree that bull age did. Bull age explained over twice
as much of the variation in conception dates as any of the other 3 variables measured. If condition influenced the timing of conception to a significant degree, we would expect earlier conceptions in years of higher herd health. However, mean conception date in 1989, when condition was highest and yearling bulls were the primary sires, was later than all other years. Cow condition was not significantly different between 1989 and 1991, yet mean conception was significantly earlier when cows were bred by 3-year-old bulls in 1991 compared with yearling bulls in 1989.

Squibb et al. (1986) hypothesized that hunting pressure (1.2–1.4 hunters/km²) during October elk and deer seasons was responsible for an observed interruption in the rut. We did not observe the near cessation of conception that Squibb et al. (1986) reported, although we observed delayed conception dates in 1989 when yearling bulls were the primary breeders (Fig. 1). We do not feel that hunting pressure contributed to the distribution of conception dates in our study. Hunting pressure was relatively light (0.9 hunters/km² in 1989) and was directed at mule deer (Odocoileus hemionus) rather than bull elk. The drop in conceptions occurred about 6 days after the start of the deer season (Fig. 2), which began on 30 September. The interval between peak frequencies in conception dates was

![Graph](image)

**Fig. 2.** Cumulative percent conceptions for adult cow elk (12 yr) bred by bulls of 5 different ages at Starkey Experimental Forest and Range, Oregon, 1989–93. The age of breeding bulls increased each year from yearlings in 1989 to 5-year-old bulls in 1993.

<table>
<thead>
<tr>
<th>Year</th>
<th>Bull age</th>
<th>1</th>
<th>2</th>
<th>3–13</th>
<th>&gt;13</th>
<th>2–13</th>
<th>n</th>
<th>n²</th>
<th>n³</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>23</td>
<td>26</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>1990</td>
<td>2</td>
<td>4</td>
<td>10</td>
<td>5</td>
<td>6</td>
<td>24</td>
<td>27</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>1991</td>
<td>3</td>
<td>2</td>
<td>8</td>
<td>5</td>
<td>5</td>
<td>19</td>
<td>21</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>1992</td>
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<td>0</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>23</td>
<td>24</td>
<td>0</td>
<td>2</td>
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<tr>
<td>1993</td>
<td>5</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>25</td>
<td>26</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

*Age grouping used for analysis.

b No. of uteri examined.

Table 3. Pregnancy rates among age classes of cow elk at Starkey Experimental Forest and Range, Oregon, 1989–93.
Table 4. Mean condition (KFI) of adult cow elk (≥2 yr old) in December by pregnancy and lactation status at Starkey Experimental Forest and Range, Oregon, 1989–93.

<table>
<thead>
<tr>
<th>Year</th>
<th>All cows</th>
<th>Pregnant</th>
<th></th>
<th></th>
<th></th>
<th>Nonpregnant</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SE n</td>
<td>Lactating</td>
<td>Nonlactating</td>
<td>SE n</td>
<td>Lactating</td>
<td>Nonlactating</td>
<td>SE n</td>
<td>Lactating</td>
<td>Nonlactating</td>
</tr>
<tr>
<td>1989</td>
<td>227*</td>
<td>19 27</td>
<td>202 21 17</td>
<td>315 31 7</td>
<td>118 1</td>
<td>190 9</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td>162b</td>
<td>13 27</td>
<td>128 11 15</td>
<td>210 29 9</td>
<td>188 13</td>
<td>3</td>
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<td></td>
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<td>1991</td>
<td>182ab</td>
<td>16 30</td>
<td>165 20 16</td>
<td>225 28 11</td>
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<td>3</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>1992</td>
<td>142c</td>
<td>16 29</td>
<td>111 18 16</td>
<td>220 20 10</td>
<td>50 5</td>
<td>3</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>1993</td>
<td>170d</td>
<td>14 32</td>
<td>133 10 17</td>
<td>217 24 14</td>
<td>155 1</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

* Means with dissimilar letters were different (P < 0.05).

about 21 days, 1 estrous cycle in elk (Morrison 1960).

Bull age may have little effect on pregnancy rates of adult cow elk given conditions similar to those at Starkey (i.e., high bull:cow ratios, high cow condition). Although pregnancy rates of cow elk at Starkey increased linearly from 1989 to 1993, it is not clear that bull age was responsible. Pregnancy rate in 1989 (89%) with yearling bulls as the primary breeders was similar to that reported by Follis (1972) (86%), also with breeding by yearling bulls. Hines et al. (1985) found higher pregnancy rates in populations dominated by older bulls; however, differences in cow condition negated their ability to evaluate effects of bull age. We were unable to document an effect of bull age on pregnancy rates partly because cow condition at Starkey exceeded what may be a threshold value for elk conception. Trainer (1971) indicated that at KFI <60, condition of Roosevelt elk becomes important in predicting pregnancy. He documented pregnancy rates for cows age 3–10 of 50% at KFI between 30 and 59, and 93% at KFI >60. KFI in 136 of 147 cases (93%) at Starkey exceeded 60. The pregnancy rate for the 11 cows in our study with KFI <60 was 82%, however, compared with 50% reported by Trainer (1971).

The demand on breeding bulls may increase in years of high cow condition because a higher proportion of cows may enter estrous (Hines et al. 1985). The age at puberty for bulls also fluctuates with condition (Hines et al. 1985). Therefore, we believe that the pregnancy rates observed in 1989, when animal condition was high, may represent near maximum breeding potential of yearling bulls.

The bull:cow ratios increased (Table 1) because we did not employ the aggressive bull removal techniques used in 1989 to remove all younger bulls from Starkey. However, we do not believe this confounded interpretation of results for several reasons. Older males dominate harem formation, and younger bulls are relegated to subordinate roles and disassociate from the harem (Prothero et al. 1979). Differences in the breeding success of red deer (C. e. elaphus) stags are closely related to fighting ability during the rut (Clutton-Brock et al. 1979), which is positively correlated with body weight and size (Clutton-Brock et al. 1982). Pemberton et al. (1992) suggested that few red deer calves were fathered by bulls without harems in a population with a bull:cow ratio of 40–60:100. Breeding by younger bulls in populations with a high proportion of older bulls apparently is negligible for red deer (Clutton-Brock et al. 1979, Gibson and Guinness 1980). Squibb (1985) reported that although bull elk older than yearlings were <25% of the total bulls available for breeding, they performed >70% of the completed copulations. Also, the peak of the rut at Starkey when bulls were ≥3 years of age was similar to that observed in Colorado (Freddy 1987) and Alberta (Flook 1970) with bull:cow ratios >40:100, indicating our study animals were performing similarly to populations with higher bull:cow ratios. Our high pregnancy rates were similar to pregnancy rates of 94% for cows 2–13 years old in populations with high numbers of mature bulls (Flook 1970).

The significant effect of bull age on conception dates in our study may have implications regarding calf survival. Timing of conception and consequent birth date affects survival of red deer calves (Guinness et al. 1978, Clutton-Brock et al. 1987), bighorn sheep lambs (Ovis canadensis) (Festa-Bianchet 1988), and presumably other ungulates in areas where predation occurs or forage quality is seasonally limited (Ginsberg and Milner-Gulland 1994). Mortality of red deer
calves increased by 1% for each day the calf was born after the median birth date (Clutton-Brock et al. 1987).

Influences of predation on calf survival may be greater in ungulate populations where the rut (and thus parturition) occurs over an extended time than in populations where parturition is more compressed. If synchronous births are effective in predator swamping, reduced synchrony in follower species may lead to increased juvenile mortality (Kiltie 1988). Wildebeest (*Connochaetes taurinus*) calves born after the peak of calving appear to have higher mortality rates, apparently due to predation (Estes 1976, Estes and Estes 1979). Our data suggest that net productivity may be enhanced by maintaining older bulls in elk populations, although the implications of birth synchrony in higher species like elk are not clear. Smith (1994) did not find higher mortality in late-born elk calves on the National Elk Refuge in Wyoming, where supplemental winter food was provided.

Bull age may also influence long-term reproductive success of cow elk. We observed a 3-week difference in the date by which 90% of the pregnant cows were bred in comparing breeding by yearling and 5-year-old bulls. Reproductive success of female red deer may decline 36% if conception is delayed 1 estrous cycle (Ginsberg and Milner-Gulland 1994). Females that give birth to late-born calves have less time to recover from the energetic demands of lactation and may not ovulate early in the rut (Laflamme and Connor 1992). Energetic demands for lactation peak 3–7 weeks following parturition (Robbins et al. 1981, Nelson and Leege 1982). In northeast Oregon, quality of forage may not be adequate to meet lactational demands of cows after late July (Irwin et al. 1994).

In northeast Oregon management units adjacent to our study area, mean conception dates typically are late (Trainer 1986), similar to those when yearling and 2-year-old bulls were the primary sires in our study. Our data suggest the low numbers of mature bulls (Trainer 1986, Schommer 1991) account for this occurrence, and in turn may contribute to low calf:cow ratios for this region. Bull age probably is not the sole reason that calf:cow ratios have declined in northeast Oregon. The delay in conception may interact with forage quality and/or predation to reduce calf survival and net productivity. More research is needed to determine bull:cow ratios necessary for early and synchronous breeding (in progress at Starkey) and to quantify the effects of calf birth date, summer and winter nutrition, and predation on calf survival.

**MANAGEMENT IMPLICATIONS**

Our results suggest that elk populations require older bulls to ensure short and early calving seasons. With this management objective, hunting regulations should be designed and habitat managed to ensure sufficient bull escapement. Relying on 2-year-old bulls to breed, a situation that results from spike-excluded hunting seasons, may not enhance herd productivity if most 2-year-olds are harvested the following hunting season. An alternative hunting strategy to increase the number of older bulls is spikes legal/branch-antlered bulls by permit hunting seasons (Vore and DeSimone 1991).

The mature bull:cow ratio required in free-ranging populations for early and synchronous breeding is unknown. Bubenik (1985) suggested 25:100, while Hines et al. (1985) speculated that 6:100 would be sufficient for high pregnancy rates and early and synchronous breeding. In our study, we observed early, synchronous breeding and high pregnancy rates with 18 3-year-old bulls per 100 cows.

**LITERATURE CITED**


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DEMOGRAPHIC PATTERNS AFTER AN EPIZOOTIC OF KERATOCONJUNCTIVITIS IN A CHAMOIS POPULATION

Anne Loison, URA CNRS 2055, UCB Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

Jean-Michel Gaillard, URA CNRS 2055, UCB Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France

Jean-Michel Jullien, Office National de la Chasse, CNERA Faune de montagne, 85 bis avenue de Wagram, 75017 Paris, France

Abstract: Data on short- and long-term consequences of epizootics on population dynamics are needed to understand limiting processes in populations and to establish management rules for hunted species. We studied a chamois (Rupicapra rupicapra) population in the French Alps that was affected by an epizootic of keratoconjunctivitis in 1977. This epizootic and the removal of 122 infected chamois led to a 37% decrease in population size. We investigated the short-term (i.e., 1977–81) and long-term (i.e., 1982–93) effects of the epizootic on reproductive parameters, finite rate of increase, and body mass. Reproductive performance and finite rate of increase climbed from 0.67 and 1.08 between 1977 and 1981, and to 0.86 and 1.13 between 1982 and 1993. Whatever the age, mass of males born during 1977–81 was lower than mass of those born after 1982 (P < 0.01), suggesting a long-term cohort effect. In the absence of hunting and removals, the population would have recovered its pre-epizootic size, reproductive parameters and rate of increase in about 5 years. We discuss the relation between population density and keratoconjunctivitis outbreaks. Because of little knowledge of transmission routes and of the host-pathogen system, and because keratoconjunctivitis is not a threat for chamois conservation, we suggested adoption of a posteriori management rules rather than rules aimed at disease prevention.

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Epizootics are difficult to study in natural populations, but can play an important role in population dynamics (Scott 1988, Hobbs and Miller 1992). Most diseases that have been investigated in wild populations concerned human health (e.g., rabies; Carey and McLean 1983, Smith and Harris 1991), or serious management and conservation problems (e.g., myxomatosis, Ross and Tittensor 1986; malaria, Var Ripper et al. 1986; or bovine tuberculosis, Anderson and TrewHELLA 1985, Cheeseman et al. 1988). However, data and models are lacking for a view of the role of different kinds of diseases in natural populations (McCallum and Scott 1994). Although population density, physiological condition, or weather, are sometimes involved (Knolle 1989, Anderson 1991), epizootics often appear to be random events (Scott 1988), mainly because pathogenic agents and transmission routes are seldom identified. Moreover, complex interactions occur between pathogens and hosts (Wakelin 1994) that are difficult to study and predict in wild populations (McCallum and Scott 1994), such as development of host immunity or reciprocal mutations in the host and the pathogen (Knolle 1989, Anderson 1991). The influence of epizootics on population dynamics is thus little understood, except for a small number of cases (e.g. Hobbs and Miller 1992, Anderson and TrewHELLA 1985), because