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Population Regulation of the Jackson Elk Herd

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POPULATION REGULATION OF THE JACKSON ELK HERD

by
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From 1990-1992, 164 neonatal elk (*Cervus elaphus*) calves were captured and radio-collared in Grand Teton National Park (GTNP) and the Bridger-Teton National Forest (BTNF) of northwest Wyoming. The elk were monitored with radio-telemetry through April 1994 to evaluate seasonal distributions and survival, causes of mortality, juvenile dispersal, and relationship of harvests to migratory patterns. The overall objective was to determine any significant differences in regulation of the relatively high densities of elk in GTNP and the elk that summered in the other three herd segments of the Jackson elk herd.

Densities of elk on calving areas (GTNP and BTNF) did not affect mortality rates of neonates. However, more males were born on BTNF than in GTNP; and neonatal mortality was male-biased due to predation, primarily by black bears (*Ursus americanus*). Annual survival rates of both calves and elk $\geq$1-year-old were higher among females than males, but survival was unrelated to the ranges on which elk summered. Recruitment rates, as measured by mid-summer

calf:cow ratios, also did not differ between GTNP and the other summer ranges.

Twenty-three percent of yearlings and 2-year-olds dispersed among the herd segments. Dispersal into GTNP, which was male-biased, exceeded the rate of dispersal out of GTNP, which was female-biased. However, hunting significantly altered the role that dispersal played in regulating the herd segments, resulting in no difference in the net rates of dispersal into and out of GTNP.

Timing of fall migrations were correlated with 10 November snow depths and annual forage production. Mean annual arrival of the GTNP herd segment at winter range preceded arrival of the other herd segments by 11-29 days each fall.

The absence of differences in the causes of mortality and rates of survival, recruitment, and dispersal suggests that the numbers of elk occupying GTNP and the other three herd segments were regulated similarly. Winter food supplementation and human predation of elk likely limit resource competition and contribute to this situation.

Chapter 6

SUMMARY AND RECOMMENDATIONS

This study investigated population regulation of the Jackson elk herd in northwest Wyoming. During 1990-1993, 164 neonatal elk were captured, radio-collared, and radio-monitored. Hypotheses were tested to ascertain any differences in reproduction, juvenile survival (neonatal, first fall, first winter, and survival of elk $\geq$1-year-old), recruitment, and dispersal of juvenile elk that summered in Grand Teton National Park (GTNP) and elk that summered outside GTNP in Yellowstone National Park, the Teton Wilderness, and the Gros Ventre drainage.

All four summer herd segments of the Jackson elk herd are hunted during fall. Because this is the primary source of mortality among the adult elk (Boyce 1989, Smith and Robbins 1994), I evaluated relationships of harvests to overall mortality and to regulation of the various herd segments.

Eighty to ninety percent of the Jackson herd is supplementally fed at the National Elk Refuge (NER) and three feedgrounds to the northeast in the Gros Ventre drainage. Winter mortality of food-supplemented elk is low (Smith 1985, Boyce 1989:144). Therefore the influence of winter food supplementation on herd regulation was also investigated.

Sex-bias in reproduction and survival can significantly influence growth of an ungulate population (Caughley 1977, Medin and Anderson 1979). Gender differences in each of the investigated regulating mechanisms were measured. This included evaluation of factors influencing sex ratios at birth.

In this chapter I summarize and integrate the research results from the previous five chapters. The diverse topics studied are ultimately interconnected and are considered collectively here to examine the overall objective of this research: Are there significant differences between population regulation of the elk that summer in GTNP and elk of the other three herd segments? Table 1 is a synopsis of the research findings as they relate to this objective and to factors affecting sex ratios. Table 2 shows which environmental variables influenced regulating mechanisms and migrations of the elk. This summary of research findings is followed by recommendations for future research and management.

Vital Statistics of Captured Calves

Survival rates of red deer and elk have been positively linked to birth weights (Albon et al. 1987, Clutton-Brock et al. 1987b, Oldemeyer et al. 1993, Singer et al. 1994). Because several of the hypotheses I tested concerned survival rates of offspring, I evaluated variation in birth weights. Birth weights were unrelated to elk densities on winter or summer ranges and to winter feeding regimen. Cohort birth weights were not different between calves born in the high density calving areas of GTNP and the relatively lower density areas outside the park.

Ninety-eight percent of the measured annual variation in cohort birth weights was explained by mean monthly December, January and March temperatures. Warmer December and January temperatures likely reduced weight loss in cows during winter allowing them to allocate less energy to recovery of body condition during the third trimester of gestation and more to fetal growth. Growth of high quality green forage in spring was dependent on snowmelt, which varied annually with March temperatures.

As reported for red deer (Blaxter and Hamilton 1980, Clutton-Brock et al. 1982a) and elk (Schlegel 1976, Singer et al. 1994), male calves weighed more than females. I also found that males were born later than females and experienced greater rates of gain during the first week of life. The high rates of gain I measured in both sexes of Jackson neonates may reflect a benefit of supplemental feeding on reproductive biology.

The larger male birth weights and rates of gain corroborate the greater parental investment in male than in female offspring reported by others (McEwan 1968, Maynard Smith 1980, Clutton-Brock et al. 1981). Given these sex-biased energetic advantages, I expected males to have higher survival than female calves.

Mortality, Survival and Recruitment Rates

Mortality of calves occurred during three periods, neonatal (birth to 15 July, 15.2%), fall (10 September-30 November, 15.3%), and winter (1 January-15 May, 16.5%). Mortality of individual calves was unrelated to birth weights. However, cohort winter survival varied positively with cohort birth weight and early-born calves suffered lower winter mortality than late-born calves, as reported by Albon et al. (1987).

Densities of elk on calving areas (GTNP vs. Bridger-Teton National Forest) did not affect neonatal rates of mortality of males, females, or the sexes combined. However, significantly more males were born on Bridger-Teton National Forest than in GTNP and neonatal mortality was male-biased. The higher mortality of males was a result of higher predation rates on males than females, primarily by black bears.

Annual survival rates were higher among female calves (0.662) than male calves (0.0502, $P < 0.05$), and among females $\geq$1-year-old (0.890) than among males $\geq$1-year-old (0.714, $P < 0.02$). Annual survival of elk $\geq$1-year-old (0.826), only one of which died of causes unrelated to hunting, exceeded ($P < 0.01$) annual survival of calves (0.579).

Survival of all ages classes was similar between the GTNP herd segment and all other herd segments. Recruitment rates, as measured by mid-summer calf:cow ratios, also did not differ between GTNP and the other herd segments.

I found lower harvests of radio-collared elk that summered outside GTNP (16%) than occurred 10 years ago (24%), and higher annual survival rates of radio-collared elk $\geq$1-year-old throughout the Jackson herd (males = 0.714, females = 0.890) than during 1978-84 (males = 0.630, females = 0.778) (Smith and Robbins 1994). Concomitantly, the size of the

Jackson estimated 7,600 elk during
winter ng winter 1992-93.

Dispers

Twenty-th ings and 2-year-olds dispersed
among th persal rate was no different
among tho Three-year-olds did not
disperse. es had significantly higher
mortalit an those that did not disperse
to new su

Dispersa was female-biased, was no
different spersal into GTNP, which was
male-bias g significantly altered the
effect tion of the herd segments.
Yearling GTNP suffered much higher
hunting ngs that dispersed out of the
park.

Fall depar anges were synchronous among
the four ever, durations of migration to
winter ran to the NER, where 87% of the
radio-colla increased with the distance
between NER. Mean arrival of the GTNP
herd segm preceded mean arrival of the

other herd segments by 11-29 days annually. This provided an opportunity to harvest primarily the GTNP herd segment in advance of arrival of the other herd segments in hunting units of GTNP and the NER. The effect of weather on annual forage production and availability during fall correlated with arrival of elk at the NER.

The absence of differences in survival, recruitment and dispersal rates suggests that significant differences did not exist in the processes regulating numbers of elk occupying the GTNP herd segment and the other three herd segments of the Jackson elk herd. Winter food supplementation and human predation rates on the GTNP elk likely limit resource competition and contribute to this situation.

Winter Distributions

Boyce (1989:42-46) reported that total January precipitation was the best predictor of annual feedground attendance by elk on the NER. I found significantly higher calf:cow and spike:cow ratios occurred off feedgrounds than on feedgrounds ($P < 0.001$). The disparity in calf:cow ratios positively correlated with the number of elk remaining off feedgrounds, the initiation date of supplemental feeding, and January weather conditions.

In addition, distributions of calves along migration routes and on winter ranges were sex-biased. More females than expected migrated along western migration routes through GTNP ($P = 0.049$), were harvested in GTNP and NER ($P = 0.07$), and wintered on the NER ($P = 0.008$). Winter mortality of calves that were food supplemented in winter was lower than mortality of those that were not supplemented ($P < 0.05$).

Research Recommendations

1. The role of dispersal in regulation of the Jackson herd segments needs further investigation. Based on the high fidelity (98%) of adult Jackson elk reported by Smith and Robbins (1994), I would expect juveniles to disperse independently of their mothers. However, fidelity of adult elk to herd segments may have declined since 1984 due to the increased density of elk in the Jackson elk herd. I recommend capture and radio-collaring of neonate-dam pairs to better understand the role of parental training in seasonal range fidelity and dispersal. This information will expand our understanding of why elk disperse, including the role of orphaning, and the relationship of juvenile dispersal to the social status and condition of dams.

2. During 1993 and 1994, activity of grizzly bears (Ursus arctos) in the eastern portions of GTNP (Hunting Unit 79) and adjacent lands on the Bridger-Teton National Forest increased. Significant bear predation on domestic livestock occurred, and in 1994 calf:cow ratios of elk declined from ratios during the previous 4 years ($P < 0.05$). On 16 August 1994, the U.S. Fish and Wildlife Service formally proposed the release of gray wolves (Canis lupus) into the Yellowstone Ecosystem, under the nonessential experimental population provision of the Endangered Species Act (section 10(j)). This action will reestablish a significant predator of elk in the Jackson herd unit. Given these recent events, a repetition of this study would provide valuable information on rates of elk predation by grizzly bears and wolves, predation competition with black bears, coyotes and mountain lions, and the possible influence of grizzlies and wolves on regulation of herd segments of the Jackson elk herd.

Winter predation of calves by wolves may be partially compensatory with winter losses due to malnutrition and disease, as suggested by Singer et al. (1993) in YNP. However, in YNP's northern range, where black and grizzly bear densities were similar, grizzlies accounted for 11-15 neonatal predations compared to only one predation by a black bear, suggesting competitive exclusion by grizzlies (Singer et al. 1994). Likewise, competitive exclusion of coyotes by wolves could render wolf predation on neonatal elk partially compensatory. These hypotheses should be tested after wolf reestablishment.

3. The male-biased sex ratio of neonates captured outside GTNP in this study, was based on a relatively small sample of calves (*n* = 39). A larger sample of calves should be captured outside GTNP to validate these results. A sightability model is currently being developed for aerial summer censusing of the Jackson elk herd (C. Anderson, University of Wyoming, unpubl. data). The model will provide maximum likelihood estimates of elk densities across the Jackson herd unit. In concert with obtaining more precise estimates of elk densities on calving areas and summer ranges, further testing of the Trivers and Willard (1973) hypothesis of adaptive sex ratios could be conducted, logically while carrying out research recommendations 1 and/or 2.

4. Sampling of vegetative biomass production and utilization in GTNP should continue for 5 more years to

verify their influence on elk migrations from GTNP under a greater range of conditions. The models developed in this research to predict the timing of elk migrations should be refined with the additional years of data.

Management Recommendations

1. Monitoring of radio-collared elk proved to be an accurate index of the Jackson herd's fall migration. Refuge herd counts were highly correlated with arrival of radio-collared elk. Because the timing of migrations vary annually, the present practice of closing the Refuge hunt when 80% of the radio-collared GTNP elk have arrived at the NER should be continued into the future. This will require monitoring sufficient numbers of radio-collared elk annually.

2. Refuge hunts should continue and should be designed to primarily harvest the GTNP herd segment of the Jackson elk herd for the following reasons:
   - Nearly all the elk that summer in GTNP winter on the NER and approximately half the elk that winter on the NER summer in GTNP (Smith and Robbins 1994).
   - GTNP elk migrate directly from GTNP to the Refuge. The limited areas in GTNP and the NER open to hunting are

the only locations where the GTNP herd segment can be harvested.

- There is only a 2-3 week period in which GTNP elk can be harvested in significant numbers in either the park or the refuge.
- GTNP elk are the earliest migrants to the NER and consume forage intended for winter use.
- Elk from the other herd segments summer on national forest lands and/or migrate across national forest lands where they can be harvested before reaching the NER (if they winter on the Refuge; many winter elsewhere in the herd unit). There is substantial opportunity to harvest those elk elsewhere in the herd unit and in a more recreational setting.
- The NER hunt should close after 80% of the GTNP herd segment has arrived to promote good distribution of forage use on the northern half of the Refuge before snow accumulations reduce availability of herbaceous vegetation.

3. The GTNP elk reduction program should be continued. At current densities and under the prevailing supplemental feeding program, there is no difference in the regulatory processes affecting elk of the GTNP herd segment and the other herd segments of the Jackson herd.

4. Changes in hunting season designs have equalized harvests and survival of the GTNP herd segment and the other herd segments. This represents a change from a decade ago when survival of GTNP elk was significantly greater than survival of elk of the other herd segments (Smith and Robbins 1994). The state and federal wildlife management agencies' goal of restoring historic (pre-1950) migrations and numbers of elk to the eastern portions of the Jackson herd unit have largely been achieved. However, the Jackson herd is now 3,000-4,000 elk above the Wyoming Game and Fish Department's herd size objective owing to larger numbers of elk in the western portions of the herd unit.

Results of this study suggest that at current densities the size of the GTNP herd segment is unlikely to be regulated by density-dependent processes. As recommended by Smith and Robbins (1994), achieving long-term change in the winter distribution of the Jackson herd offers the best opportunity to control the GTNP herd segment and the total Jackson herd size. Smith and Robbins (1994) outlined methods by which the Jackson elk herd size could be controlled without doing so at the expense of the Gros Ventre and Teton Wilderness herd segments. This research reinforces many of their recommendations, including management actions to reduce numbers of elk in the western half of the herd unit, particularly in GTNP and the NER (Smith and Robbins 1994).

Table 1. Population regulatory differences between the sexes and between the relatively high density calving areas and summer range in Grand Teton National Park (GTNP) and the lower density calving areas and summer ranges outside GTNP. The chapter where each topic is addressed appears in parentheses.

Differences Between the Sexes	Measurement	Differences Between Areas
Males born later and heavier	Vital statistics of captured calves (2)	None detected
Male-biased due to higher predation	Neonatal mortality (3)	None detected
None detected	Fall calf mortality (3)	None detected
No difference overall but sex-biased by winter range	Winter calf mortality (3)	No difference detected between the summer ranges but lower among winter supplemented elk
None detected	Annual calf mortality (3)	None detected
Male-biased	Mortality of elk $\geq$1-year-old (3)	None detected
	Recruitment rate (3)	None detected
Male-biased into GTNP and female-biased out	Dispersal rates (4)	No difference overall; greater rate into GTNP among yearlings
None detected	Mortality of dispersing elk (4)	Higher than in non-dispersers
Male-biased off the NER[a]	Winter calf distributions (4)	GTNP calves are more likely to winter on NER than other calves; calf:cow ratios are higher off the NER[a]
None detected	Timing of migrations (5)	GTNP elk arrived earlier at winter range than other elk
Male-biased among elk $\geq$1-year-old	Harvests of migrating elk (5)	None detected

[a] National Elk Refuge

Table 2. Factors that correlated positively (+) or negatively (-) with each of the measurements related to population regulatory processes. The chapter where each topic is addressed appears in parentheses.

Weather Factors	Measurement	Other Factors
December snow depth (+), mean December and January temperatures (+)	Cohort sex ratio (i.e. proportion of males/cohort) (2)	Starting date of winter feeding (+), number of elk on the NER (+)
December, January, and March temperatures (+)	Cohort birth weight (2)	Starting date (+), and ending date of winter feeding (-), and number of days of feeding (-)
	Neonatal mortality (3)	
Combined December and January precipitation (+)	Calf winter mortality (3)	Birth date (+), cohort birth weight (-), number of days of feeding (+)
January snow depths (-), January temperatures (+)	Winter calf:cow ratios off feedgrounds (4)	Starting date of winter feeding (+), number of elk off feedgrounds (+)
October precipitation (-)	Initiation of migration (5)	
10 November snow depths (-), mean July and August temperatures (-)	Arrival at winter range (5)	Herbaceous biomass produced in GTNP (+), residual biomass in high density areas of GTNP (+)