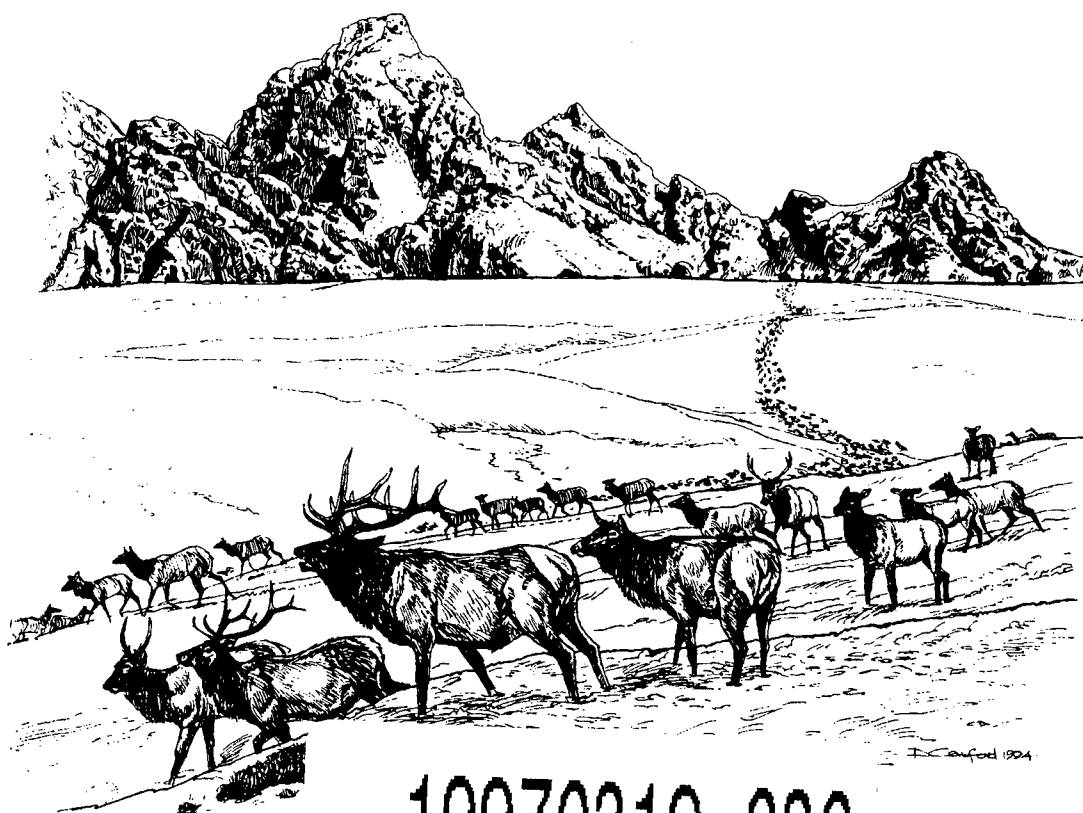


Migrations and Management of the Jackson Elk Herd

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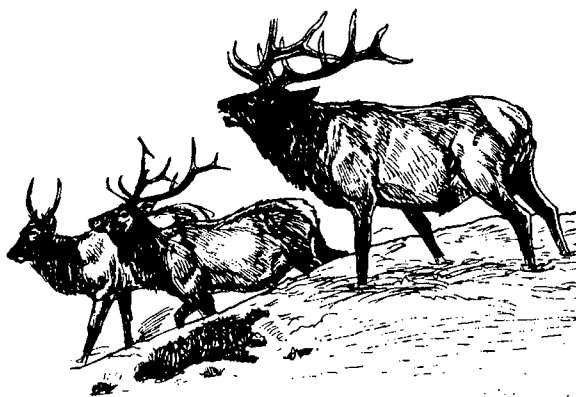
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Migrations and Management of the Jackson Elk Herd

By Bruce L. Smith
Russell L. Robbins



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Foreword

The Jackson elk herd is one of the large elk herds in the Greater Yellowstone Ecosystem and has gained international recognition and caused considerable debate. The recognition is based on the long tradition of research that began in 1927 with the assignment of Olaus Murie to the National Elk Refuge for the explicit purpose of conducting research on elk. Much of the data Murie collected was used in his book *The elk of North America*, the first comprehensive book on that topic.

Russell "Buzz" Robbins assumed Murie's position of biologist with the National Elk Refuge in 1968. He conducted research on methods for improving the elk winter feeding program, the topic of considerable debate. A natural extension of that feeding program was to determine more precisely where the elk that winter on the National Elk Refuge spend summer and fall and how the timing of their migrations affect the harvest of these elk in fall. When Robbins assumed a position with the Arctic National Wildlife Refuge, Bruce Smith became refuge biologist. Since 1982, Smith has pursued research on the Jackson elk herd with candor and a special understanding of this large ungulate and its value to the various segments of the public.

The *Migrations and Management of the Jackson Elk Herd* presents the authors' 25-year collection of data that include one of the most comprehensive sets of available data on ungulate migrations. The authors integrated their own data not only with the literature but with the numerous management reports of the past 40 years. The work is an important and comprehensive analysis of the problems and management of one of the most controversial herds of ungulates in North America.

John L. Oldemeyer
Leader
Endangered Species Research
National Ecology Research Center
National Biological Survey

Migrations and Management of the Jackson Elk Herd

by

Bruce L. Smith and Russell L. Robbins¹

*U.S. Fish and Wildlife Service
National Elk Refuge
P.O. Box C
Jackson, Wyoming 83001*

Abstract. From April 1978 to April 1982, 85 adult (≥ 2.7 years-old) elk (*Cervus elaphus nelsoni*) were captured and radio-collared on the National Elk Refuge in northwestern Wyoming. Relocations with biotelemetry from 1978 to 1984 showed that the radio-collared elk occupied four distinct summer ranges: 48% summered in Grand Teton National Park, 28% in Yellowstone National Park, 12% in the Teton Wilderness, and 12% in the Gros Ventre drainage. Elk that summered in a specific range are collectively a herd segment of the Jackson elk herd. The fidelity to the summer ranges was 98%; the fidelity to the winter range at the National Elk Refuge was 97%. At least 69% of the calving by elk from all four summer ranges occurred in the Grand Teton National Park central valley. The fidelity to calving areas inversely correlated with the distance between a calving area and the National Elk Refuge winter range. The fall migration commenced in October or November, and 94% of the radio-collared elk arrived at the National Elk Refuge by 15 December. Most elk that were harvested by hunters in the park and on the National Elk Refuge during the early stages of the fall migration were from the Grand Teton National Park herd segment. From 1978 to 1984, hunters reduced the number of wintering elk on the National Elk Refuge from 8,413 to 5,010. Efforts to reduce the size of the Grand Teton National Park herd segment by hunting have been unsuccessful. However, the size of this herd segment seemingly stabilized since the late 1960s and was about 3,700 elk (2,869–4,486, 95% CI, post-hunting season) during this study.

We recommend the establishment of management objectives for each of the four herd segments and an investigation of density-dependent effects on the recruitment, survival, and dispersal of juveniles. Reducing the number of elk in Grand Teton National Park and restoring the number and migrations of elk east of Grand Teton National Park to pre-1950 conditions are goals of the state and federal agencies that manage the elk and their habitat. Alternative management based on this research is offered to accomplish those goals.

Key words: Brucellosis, *Cervus elaphus*, elk, harvest, management, migration, survival, Wyoming.

¹ Present address: Route 2, Box 50, Elk Point, South Dakota 57025.

The management of the Jackson elk (*Cervus elaphus*) herd in northwestern Wyoming is a complex interagency effort. The elk of the Jackson elk herd are known for their winter concentrations and extensive annual migrations (as long as 90 km) between their winter and summer ranges. They migrate through and summer in the Bridger-Teton National Forest, Yellowstone National Park, Grand Teton National Park, and scattered parcels of private and state lands (Fig. 1). Some elk winter in the Bridger-Teton National Forest and Grand Teton National Park, but about 90% of the Jackson elk

herd winters and is supplementally fed at the National Elk Refuge and at three state-operated feed grounds in the Gros Ventre River drainage (Fig. 2).

The U.S. Fish and Wildlife Service and the Wyoming Game and Fish Department work under a 1974 cooperative agreement to manage the National Elk Refuge for a maximum of 7,500 elk, which is 68% of the targeted post-hunting-season size of the entire Jackson elk herd.

By the early 1900s, fewer than 50,000 elk remained in North America. Most were concentrated in the area of Yellowstone National Park



A 9-month-old elk eating alfalfa pellets on the National Elk Refuge, Wyoming; March 1991.

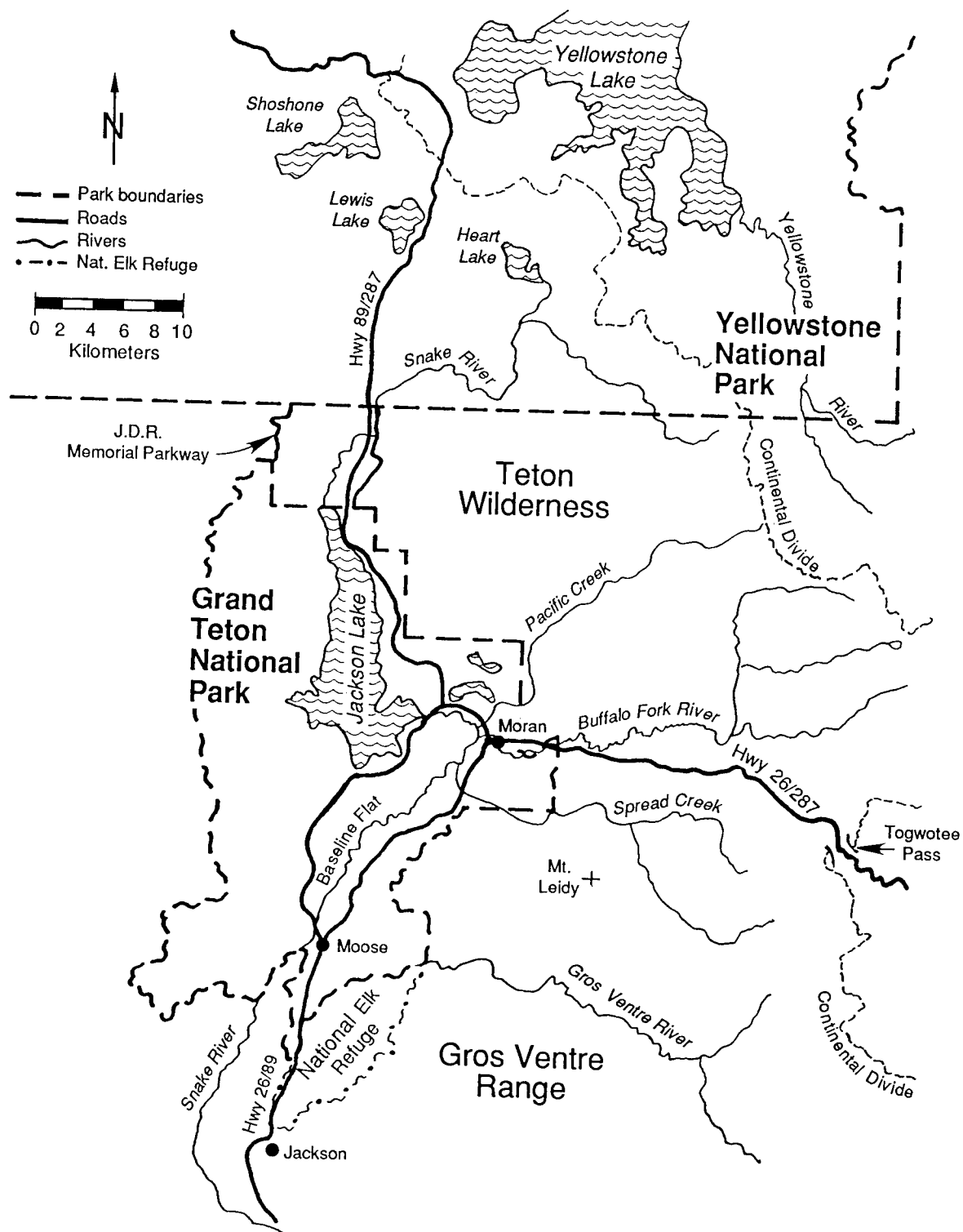


Fig. 1. The northern Jackson Hole region.

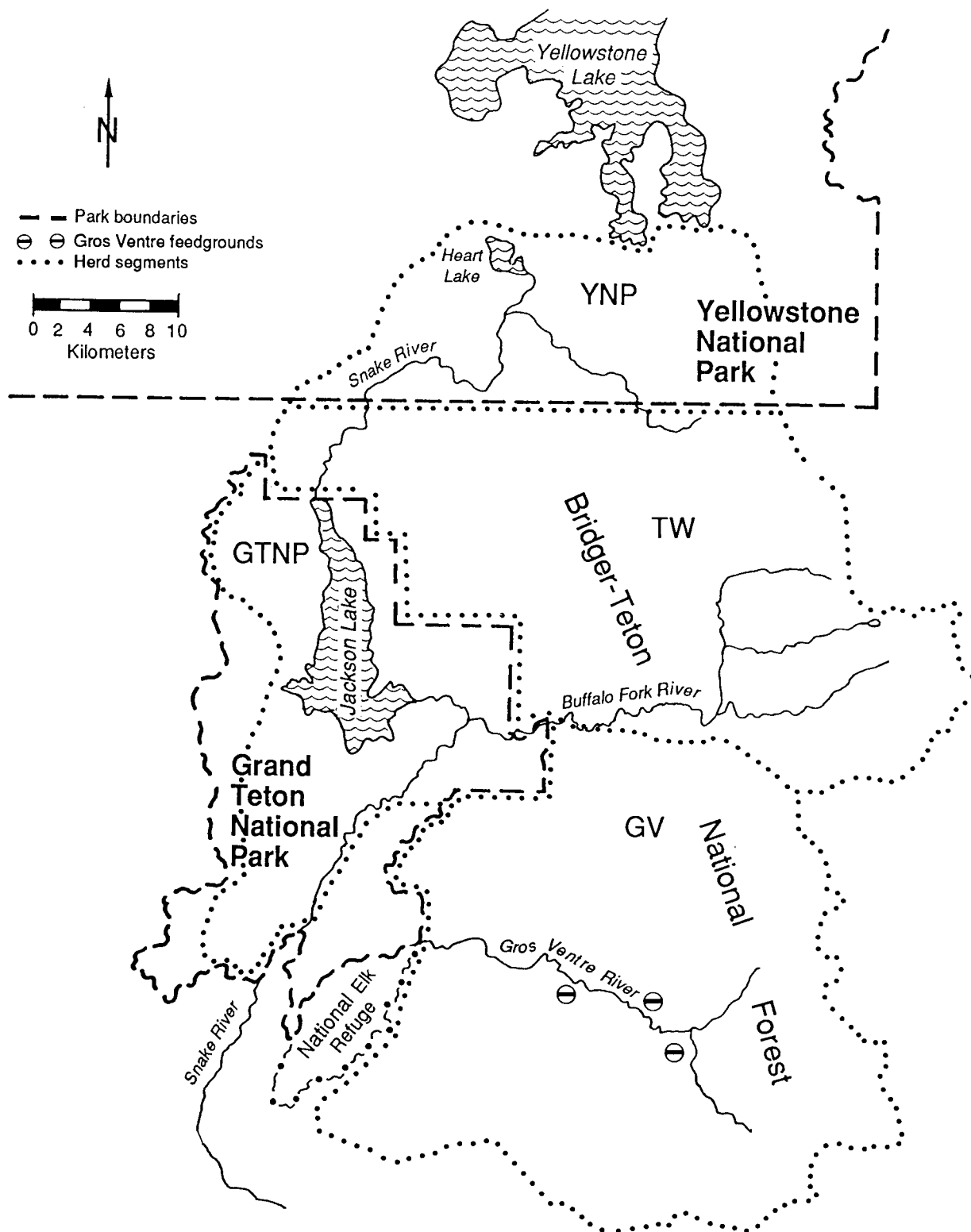


Fig. 2. Summer distributions and winter feed grounds of the four herd segments of the Jackson elk herd: Grand Teton National Park (GTNP), Yellowstone National Park (YNP), Teton Wilderness (TW), and Gros Ventre drainage (GV).

and Jackson Hole (Seton 1927). Accounts of the abundance of elk in Jackson Hole prior to European settlement in 1884 are limited to observations by fur trappers and explorers (Anderson 1958; Robbins et al. 1982). Postsettlement estimates and censuses of elk wintering in the Jackson Hole valley were made by game wardens and U.S. Forest Service personnel. Cole (1969:15) stated:

The 1887 to 1911 estimates of 15,000 to 25,000 elk in the Jackson Hole herd, with the largest numbers reported during severe winters, should establish that the Jackson Hole and Gros Ventre Valleys were historical winter areas. The first organized censuses (beginning in 1912 and covering Jackson Hole and the Hoback River drainage south of Jackson), which accounted for approximately 20,000 animals, also seem to confirm that large numbers of elk were present historically.

This statement disputes claims that elk began wintering in Jackson Hole only after settlement blocked migration routes from the valley to historic winter ranges to the south (Anderson 1958).

In 1911, the Congress authorized an investigation of the status of the elk herds in Jackson Hole (Preble 1911). Preble estimated that 20,000 elk summered north of Jackson: 8,000 between the Gros Ventre and Buffalo Fork rivers and another 12,000 north of the Buffalo Fork River of which no more than 4,000 were in Yellowstone National Park (Fig. 1).

The establishment of Yellowstone National Park in 1872 and the National Elk Refuge in 1912 were landmarks in the protection of elk from market and tusk hunting and usurpation of critical habitat for human uses. In 1912, the Congress established the National Elk Refuge as a winter range for elk in Jackson Hole. Feeding of elk in winter was initiated to mitigate losses of historic winter ranges after the settlement of Jackson Hole by Europeans in 1884 and attendant livestock grazing and haying on winter ranges. Subsequent conflicts between elk and ranchers and periodic heavy mortality of elk during severe winters typified the 1890s and early 1900s (Brown 1947; Anderson 1958; Robbins et al. 1982). Feeding of the elk in the Gros Ventre drainage during

winter was on an emergency basis until the 1950s when annual feeding operations began (Anderson 1958).

After establishment of the National Elk Refuge, the number of elk in Jackson Hole began to stabilize, although the number and probably the distribution of elk in what is now Grand Teton National Park apparently declined between 1900 and 1950 (National Park Service. 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment. Moose, Wyo. 459 pp.). Established in 1929, Grand Teton National Park originally included only the Teton Range. Cattle ranching and dude ranches (to serve a growing tourist industry) occupied the northern Jackson Hole Valley (lands north of the National Elk Refuge between the Teton Range on the west and the Gros Ventre Mountains and mountains of the Teton Wilderness on the north and east), which was added to Grand Teton National Park in 1950. This addition to the park is known as the *central valley* of Grand Teton National Park. Prior to 1950, fewer elk than now summered in the central valley (Anderson 1958; Cole 1969).

The state of Wyoming resisted expansion of Grand Teton National Park for fear that elk protected in the park would increase and predominate among the elk wintering on the National Elk Refuge and among the elk on the feed grounds in the Gros Ventre drainage (Blunt 1950) and therefore in the Jackson elk herd. Consequently the legislation (Public Law 81-787) specified that reductions of elk be permitted in designated portions of the expanded Grand Teton National Park.

The public's interest and demand for elk increased after 1950 when competing uses of elk habitat on public and private lands for timber and energy production, recreation, living space for the human population of Jackson Hole, and visitation to the area grew (C. Phillips and S. Ferguson. 1977. Hunting and fishing expenditure values and participation preferences in Wyoming, 1975. University of Wyoming, Laramie, unpublished; Rippe and Rayburn 1981; Roelle and Auble 1983). Intensified resource development in the Bridger-Teton National Forest, expanding road systems, upgrading of existing roads, increased hunting pressure, loss of winter range by development of private lands, and expansion of Grand Teton National

Park in 1950 altered the distribution and harvest of the elk.

Hunting of the Jackson elk herd has long been an attraction and a source of debate (C. Sheldon 1927. The conservation of the elk of Jackson Hole, Wyoming: A report to the President's committee on outdoor recreation and the Governor of Wyoming, unpublished; Brown 1947; Murie 1951). Some observers perceive irony in the maintenance of a population of elk at high numbers by tax-subsidized feeding and the hunting in a national park to control the size of the same population (Wood 1984). Elk hunting on the National Elk Refuge has likewise received adverse national attention (Dexter 1984). However, the mortality of the Jackson elk herd in winter is low, and hunting on those federal lands has been important to controlling the herd's size (Thomas et al. 1984; Boyce 1989). Individuals who favor hunting disagree on where and how the elk should be harvested. Some want even more elk harvested because of direct or indirect economic interests (Taylor et al. 1982; Boyce 1989).

Since the expansion of Grand Teton National Park, a growing concern of managers has been to improve the distribution of elk on summer ranges (i.e., more elk on national forest lands and fewer in Yellowstone National Park [Anderson 1958; Cole 1969]). Anderson (1958) and later Cole (1969) advocated (1) increasing harvests of the Yellowstone National Park herd segment that travelled through the roadless Teton Wilderness before crossing Grand Teton National Park because that herd segment had become too large to manage and (2) allowing compensatory increases in elk that migrated through roaded areas east of Grand Teton National Park or summered on the national forest lands between the two parks. To the present, this has included an annual elk hunt in Grand Teton National Park. Cole (1969) also urged hunting in Grand Teton National Park to control the increasing number of elk that summered there and wintered on the National Elk Refuge. The elk that summered in Grand Teton National Park were the earliest migrants to the National Elk Refuge each fall and consumed forage intended for winter grazing.

Cole (1969) estimated the proportion of the elk that wintered on the refuge and summered on various ranges in Jackson Hole during the 1960s.

His methods included (1) repeated ground and aerial counts on sample areas; (2) recording of the proportion of elk that had been neck-banded on the National Elk Refuge in winter and had been observed on various summer ranges; and (3) track counts of migrating elk along a 76-km-road transect and periodic counts of elk arriving at the National Elk Refuge. The road transect started at Moose, Wyoming, and extended north through the west side of the park to Moran, Wyoming, and then east to the top of the Togwotee Pass (Fig. 1).

Cole's (1969) analysis and Boyce's (1989) updated analysis through 1985 illustrate that the proportion of elk that migrated through Grand Teton National Park from Yellowstone National Park and the Teton Wilderness drastically increased since 1950. Because the counts do not include tracks of elk that migrate from the Gros Ventre drainage to the National Elk Refuge or tracks of all elk that summer in Grand Teton National Park, the track counts cannot be used alone to determine the proportions of elk in each herd segment. Furthermore, when they cross the road transect between Moran and the Togwotee Pass, elk of the Teton Wilderness herd segment cannot be distinguished from elk of the Yellowstone National Park herd segment. Therefore, Boyce (1989) combined the elk from the Yellowstone National Park and Teton Wilderness herd segments in his analysis. Finally, varying numbers of elk that cross the transects each year in the absence of snow do not leave tracks and are therefore not recorded.

Test results of about 28% of the elk that winter on the National Elk Refuge (39% of the adult females) are positive for *Brucella abortus* antibodies (Boyce 1989). Brucellosis, which is caused by *B. abortus*, not only affects the health and productivity of the Jackson elk herd (Thorne et al. 1991; Oldemeyer et al. 1993) but is potentially transmissible among cattle, bison, and elk (Thorne et al. 1982; Davis et al. 1988). The Jackson bison herd is also infected with brucellosis (Williams et al. 1993). Because of the cattle ranching in Jackson Hole, an understanding of the spatial and temporal overlap of seasonal ranges of the three species and potential risk of brucellosis transmission is essential to management of the Jackson elk and bison herds and to planning of grazing allotments on federal lands.

Objectives

In 1978, we initiated this study of the approximately 7,500 elk that winter on the National Elk Refuge. We monitored elk with radiotelemetry during 1978–84 to evaluate management and subsequent changes in the elk population. During the study, the number of wintering elk on the refuge declined by 40%. We had 8 objectives.

1. Determine the seasonal distributions and migrations of elk that winter on the National Elk Refuge.
2. Evaluate Cole's (1969) prediction that the cooperative management of the National Park Service and Wyoming Game and Fish Department will restore the historic (pre-1950) migrations and distributions of the Jackson elk herd by reducing the Yellowstone National Park herd segment and increasing the Teton Wilderness herd segment.
3. Identify calving locations and their relation to distributions of the Jackson elk herd.
4. Identify migration routes and timing of migrations. Fall-migration routes were described by Anderson (1958) and Cole (1969), and their relative use was estimated from track counts in the snow (Boyce 1989). We sought to determine which routes elk from the various summer ranges used and if fall migrations from all summer ranges were initiated by snow accumulations (Rudd et al. 1983, Boyce 1991).
5. Determine the degree of fidelity of elk to winter ranges, herd segments, calving areas, and migration routes.
6. Estimate the annual harvest rates of elk in each herd segment. (Rudd et al. 1983, Boyce 1991).
7. Estimate survival rates and determine whether survival rates of elk that summered inside and outside Grand Teton National Park differed.
8. Identify where distributions of elk, cattle, and bison spatially or temporally overlap.

Study Area

The Jackson elk herd roams the northern portions of an intermountain basin known as Jackson

Hole and the surrounding Teton Range to the west, Gros Ventre Range to the east, and mountains of southern Yellowstone National Park and the Teton Wilderness to the north. The Fall Creek elk herd occupies the Snake River and lower Hoback River drainages of southern Jackson Hole south of the town of Jackson. The Jackson elk herd's distribution (the Jackson herd unit) encompasses 5,195 km² in the Snake River watershed, which drains to the south, and the Yellowstone River watershed, which drains to the north (Fig. 1).

Elevations range from 1,890 m on the National Elk Refuge to more than 3,600 m in the mountains. Geologic features were described by Love and Reed (1968) and Houston (1968); the vegetation was described by Cole (1969). Plant communities include riparian cottonwood (*Populus angustifolia*) woodlands and sagebrush (*Artemisia* spp.) grasslands in the Jackson Hole valley; aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) forests in the foothills and on the lower mountain slopes; spruce (*Picea engelmannii*) and fir (*Abies lasiocarpa*) forests and tall forb meadows in the subalpine zone; and arctic alpine vegetation above 3,050 m.

The average annual precipitation at Moran, Wyoming, is 57 cm. The mean annual temperature is 1.7° C and ranges from monthly means of -11.0° C in January to 14.7° C in July (National Oceanic and Atmospheric Administration 1982). Elk that summer in the Teton Wilderness and Gros Ventre drainage occupy lands (primarily the Bridger-Teton National Forest) that are open to big-game hunting in the fall. Yellowstone National Park is closed to hunting, but elk that summer there are subject to hunting as they migrate south from the park. Elk that summer in or migrate through portions of Grand Teton National Park, in which hunting is permitted under Public Law 81-787 (the legislation for the expansion of the park in 1950), can be hunted. Those areas are also designated Wyoming Hunting Units 75, 76, and 79 and are east of U.S. Highway 89/287 and the Snake River (Fig. 3). Hunting Unit 72 in the northwest corner of the park has been closed to hunting since 1967. A limited elk hunt is held on the northern half of the National Elk Refuge, designated as State-Hunting Unit 77.

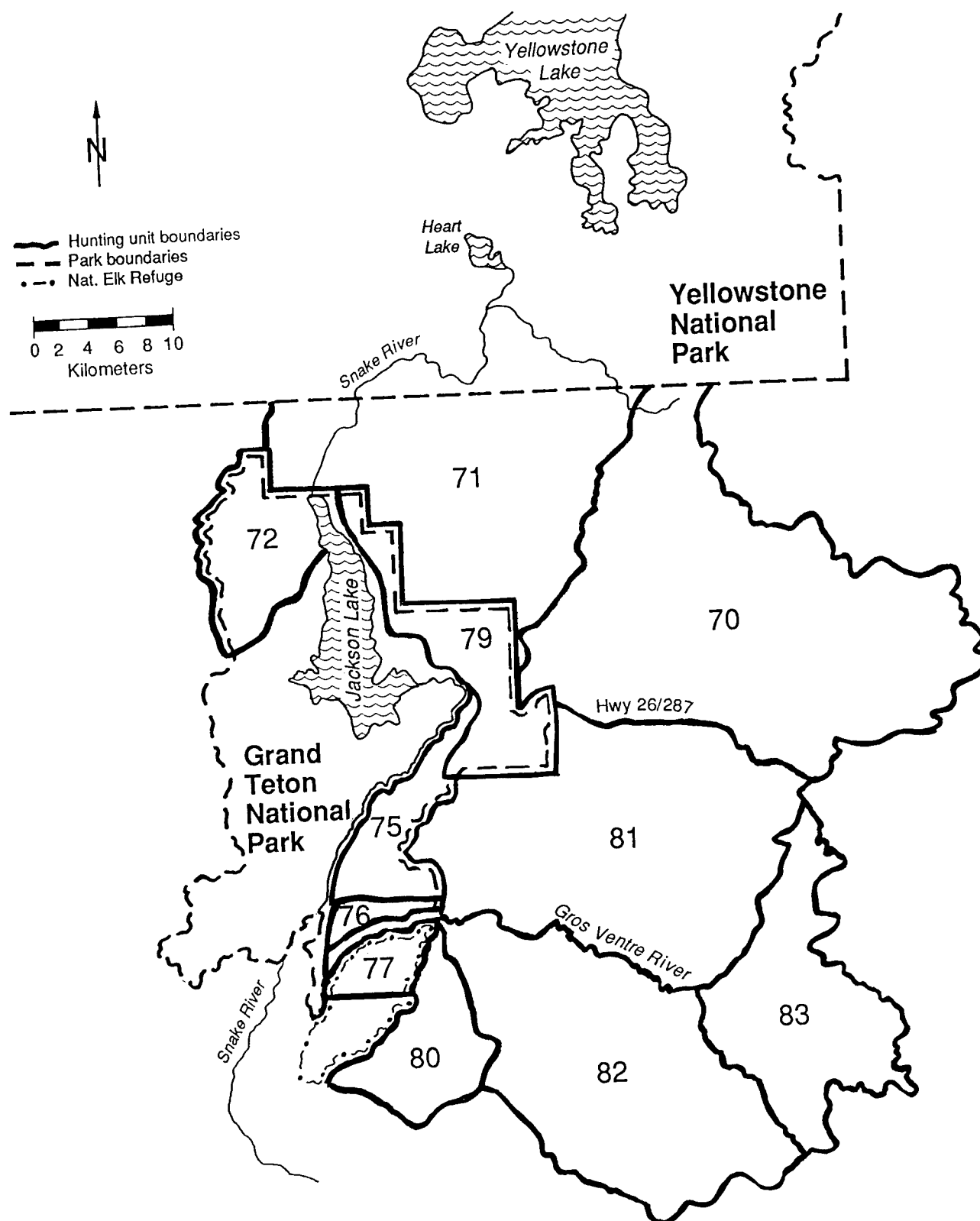


Fig. 3. Hunting units in the Jackson elk herd unit.

Methods

Definitions

The geographical range of the Jackson elk herd is 5,195 km² in the Snake River and Yellowstone River watersheds and is known as the *Jackson herd unit* (Cole 1969; Fig. 1). In summer, the Jackson elk herd separates into four *herd segments*, each of which summers on one of four ranges: Grand Teton National Park, Yellowstone National Park, the Teton Wilderness, and the Gros Ventre drainage (Fig. 2). The Grand Teton National Park summer range is divided into Northwest Grand Teton National Park and Grand Teton National Park valley. Grand Teton National Park valley refers to all lands south and east of Jackson Lake and comprises the summer range of most of the Grand Teton National Park herd segment (Fig. 1). In winter, elk of the herd segments mingle on the National Elk Refuge and on other ranges of the Jackson herd unit and 80–90% are provided with supplemental feed on *feed grounds*.

Capture of Elk for Radio-Collaring

During early April of the years 1978–82, 76 pregnant, ≥ 2.7 year-old elk were radio-collared and released. These females were obtained from those used in feeding trials on the National Elk Refuge to determine maintenance rations of winter feed for elk (Oldemeyer et al. 1993). After the elk were captured in a baited corral trap, they were placed in 2- or 4-ha pastures. Their ages were determined from tooth eruption and wear (Quimby and Gaab 1957). Pregnancy was determined by palpation of recta (Greer and Hawkins 1967). In 1978, 1979, and 1980, every other female elk was radio-collared and released during April when all elk in the feeding trials were retrapped for weighing. In 1982 (trials were not conducted in 1981), collars were placed on only six elk in April, one on every tenth animal (Appendix A).

We captured and radio-collared another 21 ≥ 2.7 year-old elk (17 males and 4 females) during March and April of 1981 by immobilizing them with powdered succinylcholine chloride-loaded Pneu-Darts (Pneu-Dart, 406 Bridge Street, Williamsport, Pa. 17701) that we shot from trucks. We recaptured 35 elk on the National Elk Refuge with

the same technique and replaced nonfunctioning radios and radios nearing the life expectancy of the batteries. Three of the 35 elk were recaptured twice (Appendix B).

The sample of radio-collared elk is a small proportion of the elk that winter on the National Elk Refuge, and the randomness of the sample may be questioned. However, money and time constraints precluded a larger sample. We offer the following arguments that the sample was adequate for meaningful inferences.

After their arrival on the National Elk Refuge each fall, elk from the four herd segments were assumed to mingle. The arrival of the elk coincided with the elk hunt on the northern half of the refuge and with early-winter snowfall. The elk congregated in one or two large groups on the southern one-third of the refuge until the conclusion of the hunt. From then until supplemental feeding commenced in January, the elk ranged freely in dynamic groups.

We provided the elk with supplemental feed at four feed grounds that were separated from each other by 1–2 km. After each morning's feeding, the elk bedded until mid-afternoon. While grazing on the flat grasslands on the refuge during the evening and night, elk from adjacent feed grounds mingled. No physical barriers inhibited the elk from moving among the four feed grounds.

We trapped and immobilized elk at random. The trap was near the center of the refuge where elk from all feed grounds on the refuge mingled. We immobilized elk on two different feed grounds. We determined that proportions of radio-collared elk that migrated to each summer range were not different ($X^2 = 1.97$, $df = 3$, $P = 0.58$; Table 1). We therefore combined the trapped and immobilized elk in one sample for data analyses.

Subsequent monitoring indicated that radio-collared elk randomly mingled on the National Elk Refuge. The frequency of daily feed-ground attendance by radio-collared elk was not different among the three feed grounds on which elk were captured and radio-collared ($F = 0.55$; $df = 2, 56$; $P = 0.58$). Elk from all four herd segments freely traveled between feed grounds during winter.

We also compared the expected with the observed use of feed grounds by radio-collared elk on the refuge. The frequency of attendance, based on relocations with telemetry, was considered *use*,

Table 1. Numbers (n) and proportions (p) of elk (*Cervus elaphus*) of herd segments^a of the Jackson elk herd that were trapped and immobilized on the National Elk Refuge, Wyoming, 1978–1982. The proportion of trapped and immobilized elk did not differ between herd segments.

Herd segment (summer range)	Trapped		Immobilized		Test result	
	n	p	n	p	Z	P
Grand Teton National Park	29	0.45	12	0.57	-0.77	0.22
Yellowstone National Park	19	0.30	5	0.24	0.40	0.34
Teton Wilderness	7	0.11	3	0.14	-0.19	0.42
Gros Ventre Drainage	9	0.14	1	0.05	0.67	0.25

^aThe herd segments are identified by their summer ranges.

and mean daily numbers of elk at each feed ground during the study was considered *availability*. Simultaneous 95% confidence intervals were constructed around the proportions of use of the four feed grounds (Neu et al. 1974; Byers et al. 1984; Table 2). Preference was not demonstrated ($X^2 = 1.07$, $P = 0.79$). Based on these analyses, we believe that the distributions of the radio-collared elk on summer ranges provided an unbiased estimator of the overall summer distribution of the elk that wintered on the refuge.

Radio Performance

Personnel of the Denver Wildlife Research Center built the 24 radio collars placed on elk in 1978 and another 34 placed on elk in 1979 (17 replaced nonfunctioning collars from 1978). Telonics, Inc. (Mesa, Arizona) manufactured the radio collars placed on elk in 1980–82. Each elk was monitored for ≤ 60 months (Appendix A).

Embossed instructions on the radio collars requested hunters to return the collars to the National Elk Refuge and to provide information on the date and place of harvest. We retrieved collars of elk believed dead from natural causes. Ages at the time of death were determined from an analysis of the cementum annuli (Mitchell 1963).

Monitoring with Radiotelemetry

We attempted to locate transmitters 3 times/week during migration and approximately weekly at other times by triangulation with mobile ground-based receiving equipment (Appendix A). We transported the three-element yagi antennas, AVM-164-MHz receivers, and headphones by vehicle and on foot and horseback to strategic signal-receiving locations. During April–December, Cessna 182 and 206, Piper Super Cub, and Maule fixed-wing aircraft were used to locate elk. Three-element, unidirectional yagi antennas, attached to

Table 2. Confidence intervals of the observed (P^i) and expected (P^{i0})^a proportions of use of the four feed grounds on the National Elk Refuge, Wyoming, by radio-collared elk (*Cervus elaphus*) of the Jackson elk herd, 1978–1984. All confidence intervals were constructed with the Bonferroni procedure and contained the expected proportions.

Feed ground	Proportional use		95% Confidence intervals
	Observed (P^i)	Expected (P^{i0})	
Shop	0.113	0.130	0.046–0.179
Nowlin	0.310	0.300	0.213–0.407
Poverty Flats	0.296	0.317	0.200–0.391
McBride	0.282	0.252	0.187–0.376

^aByers et al. 1984.



Grazing by livestock and haying of historic winter ranges of elk in Jackson Hole, Wyoming, led to severe mortality of elk during some winters and to the subsequent supplemental feeding of the Jackson elk herd. Photo by S.N. Leek [deceased] 1909.

each wing strut and linked to a Telonics receiver-scanner and right-left switch box, were used to locate elk that migrated beyond the range of receiving equipment on the ground.

Delineation of Seasonal Ranges

Radio locations were plotted on USGS topographic maps and recorded by the Universal Transverse Mercator Coordinate System. For analyses and interpretations of summer distributions of the elk and their fidelity to specific summer ranges, we used the same geopolitical herd segment designation as the state and federal wildlife management agencies (Straley 1968; Cole 1969): Grand Teton National Park, Yellowstone National Park, Teton Wilderness, and Gros Ventre Drainage herd segments (Fig. 2). For analyses of migratory patterns, the Grand Teton National Park herd segment was subdivided into a NW Grand Teton National Park

(all lands in Grand Teton National Park west of Jackson Lake) and Grand Teton National Park valley (the remaining southern and central part of Grand Teton National Park that is the summer range of most elk of the Grand Teton National Park herd segment). Fidelity to seasonal ranges was measured as an elk's frequency of return to its previous year's winter range and its previous year's summer range. Elk were monitored for as many as 5 years. Each elk that was monitored for more than 1 year provided *opportunities* for an evaluation of its seasonal range fidelity.

We examined whether more than the expected number of yearlings (sexes combined) summered in Grand Teton National Park, as reported by Martinka (1969) during the 1960s. We compared the proportion of yearlings (sexes combined) of the harvested elk of the Grand Teton National Park herd segment with the percentage of young (<1-year-old elk) in the censuses during the previous winter at the National Elk Refuge.

Data on cattle grazing allotments, dates of permitted grazing, and number of cattle were obtained from Grand Teton National Park and the Bridger-Teton National Forest. We mapped seasonal distributions of bison from biotelemetry relocations (S. Cain, Grand Teton National Park, unpublished data) and recorded observations by personnel of Grand Teton National Park, the National Elk Refuge, and the Wyoming Game and Fish Department.

Delineation of Calving Areas

Relocations of female elk during the peak parturition period of 25 May–15 June 1978–83 (Johnson 1951; Murie 1951; Oldemeyer et al. 1993) were plotted on U.S. Geological Survey maps (1:24,000 scale) with the Universal Transverse Mercator grid system to define areas that female elk frequented during calving seasons. To estimate the proportion of the Jackson herd unit in which the radio-collared female elk calved, the number of 1-km² grid squares in which one or more females were located during 25 May–15 June were divided by the 5,195 km² of the Jackson herd unit. Because we did not always see the females that we located by radio and because radio-collared females were often with other elk, we could rarely confirm whether a radio-collared female had given birth. When a young accompanied a lone radio-collared female, we assumed the young was her offspring.

We investigated the fidelity to calving areas of females that we monitored during two or more calving seasons. To do so required delineating specific calving areas from relocations of elk. Our definition of calving areas as "the areas, usually on spring range, where females give birth to young and maintain them during their first few days or weeks" follows Thomas et al. (1979:471).

Estimated Sizes and Age-Class Compositions of Herd Segments

Estimates of the number of elk summering in Grand Teton National Park from 1963 to 1985 were made with a Lincoln-Petersen estimator developed by Martinka (1969) from mark-recapture

studies. These estimates included elk in only a portion of the Grand Teton National Park valley. Maximum counts from 2–4 repetitions each summer were expanded to provide an estimate of the total number of elk in the valley. The 95% confidence intervals are approximately $\pm 27\%$ of the estimates. Boyce (1989) recently provided an evaluation of the Martinka estimator. He concluded that the precision of the estimates seemed reasonable but the results were biased underestimates of the number of elk in the valley because of poor observability of the increasing number of adult males.

Annual classifications (young, yearling males, mature males, and females) of elk in the Grand Teton National Park central valley were routinely conducted with spotting scopes by park personnel from vantage points in the park. An evaluation of the reliability of the classification technique is forthcoming (S. Cain and B. Smith, in preparation). We also classified elk that we encountered during radio-tracking.

Annual winter censuses and classifications of elk on the feed grounds on the National Elk Refuge and in the Gros Ventre drainage were conducted in a systematic fashion from feed wagons. After hay was distributed in two long lines, the feed wagon slowly passed between the two rows of feeding elk. Young, yearling males, mature males, and total number of elk were counted by federal- and state-agency biologists and managers. The number of females was obtained by subtracting the number of elk in all other age classes from the total number of counted elk. Replicate counts of each age and sex class by the multiple observers were averaged. These counts were scheduled to coincide with the greatest attendance of the feed grounds by elk (Boyce 1989).

Evaluation of Harvests

Harvests of elk of the four herd segments was deduced from harvests of radio-collared elk. Harvest rates of elk of the Jackson herd unit were determined from radio-collared elk and also from harvest records compiled by the Wyoming Game and Fish Department, Grand Teton National Park, and the National Elk Refuge. These records are based on (1) an annual mail survey of licensed

elk hunters conducted by the University of Wyoming under contract to the Wyoming Game and Fish Department, (2) a permanent hunter check station east of the Jackson herd unit along State Highway 26/287 at Dubois, Wyoming, operated throughout the elk hunting season, and (3) mandatory reporting of elk killed by hunters that receive permits to hunt in Grand Teton National Park and the National Elk Refuge. Hunters in the park and on the refuge are either contacted by enforcement personnel in the field or must return a portion of their permit with information about the results of their hunt.

Statistical Treatment

Standard statistical procedures described by Sokal and Rohlf (1981) were used. Correlation and regression analyses were used to test relations between continuous random variables. Stepwise multiple regressions to predict fidelity to calving areas were conducted with the following independent variables: distance of calving area from the National Elk Refuge, elevation of calving area, and climatic data of calving areas near one of the four weather-reporting stations in the Jackson herd unit. Differences in means were tested with the Student's *t* test and one-way analyses of variance. Differences in frequencies and proportions were examined with chi-square and Z-test analyses. Because of the relatively small samples of monitored, radio-collared elk in any given year in any given herd segment of either gender, probabilities of Type II errors were high in hypothesis tests. When appropriate, data from years or herd segments were sometimes combined.

Maximum-likelihood survival rates of adult (≥ 2.5 year-old) elk were estimated from the biotelemetry data with the Program SURVIV (White 1983). Because elk were captured and radio-collared in March or April, annual survival rates were measured from 1 April of the year in which the animals were collared to 1 April of the succeeding years.

Standard errors (SE) of the proportions of radio-collared elk in each herd segment were calculated with the estimated variance for the binomial distribution:

$$SE = \sqrt{p(1-p)/n}$$

where p = the proportion of radio-collared elk from a herd segment and n = the total number of radio-collared elk. Because the radio-collared elk were assumed to be a random sample of the herd, the SEs were applied to estimate the number of elk in herd segments.

All point estimates of parameters are presented $\pm$ SE unless otherwise indicated. The level $P < 0.05$ was considered significant.

Results

Summer Distribution

We monitored the 97 radio-collared elk for an average of 19.2 months (Appendix A). However, 9 premature radio failures and 3 natural mortalities precluded determining the summer ranges of 12 of the 97 elk. The remaining 85 animals used all four summer ranges: 48.2% (95% CI = 37.6 to 58.8) summered in Grand Teton National Park, 28.2% (18.6 to 37.8) in Yellowstone National Park, 11.8% (4.9 to 18.6) in the Teton Wilderness, and 11.8% (4.9 to 18.6) in the Gros Ventre drainage (Table 3). The number of males ($X^2 = 8.2$, 2 df, $P = 0.02$), number of females ($X^2 = 25.1$, 2 df, $P < 0.001$), and number of the combined sexes of the radio-collared elk in each of the four herd segments were not the same ($X^2 = 30.9$; 2 df; $P < 0.001$).

Of the 85 monitored elk, $45.8\% \pm 10.6$ (95% CI) summered in areas that were closed to hunting west of the Snake River and Jackson Lake in Grand Teton National Park (Figs. 2, 3). Only 2.4% of the 85 elk summered in areas that were open to hunting (Hunting Units 75, 76, and 79; Fig. 3) in Grand Teton National Park.

Fidelity to Winter Ranges

The fidelity to the National Elk Refuge winter range was 97% (138 of 142 opportunities) among the radio-collared elk that survived one or more years. Three of the four times when elk did not return to the National Elk Refuge (but remained in the Jackson herd unit) occurred during winter of 1980–81, when snowfall was so low that

Table 3. Distributions of 85 radio-collared elk (*Cervus elaphus*) of the Jackson elk herd and the number of summers during which the elk were monitored, 1978–1984. Data are presented by herd segment, each of which is identified by its summer range.

Herd segment (summer range)	Number of monitored elk				Number of summers of monitoring									
	Male	Female	Total		1		2		3		4		5	
			n	%	M	F	M	F	M	F	M	F	M	F
Northwest Grand Teton National Park	2	4	6	7.1	1	2	1	2	0	0	0	0	0	0
Grand Teton National Park valley	7	28	35	41.2	1	11	5	3	0	4	1	5	0	5
Combined ^a	9	32	41	48.2	2	13	6	5	0	4	1	5	0	5
Yellowstone National Park	3	21	24	28.2	2	11	1	6	0	2	0	0	0	2
Teton Wilderness	4	6	10	11.8	3	2	1	0	0	4	0	0	0	0
Gros Ventre drainage	1	9	10	11.8	0	4	1	3	0	1	0	1	0	0
Total	17	68	85	100.0	7	30	9	14	0	11	1	6	0	7

^a Northwest Grand Teton National Park and Grand Teton National Park valley.

supplemental feeding was not required at the National Elk Refuge.

Fidelity to Summer Ranges

Radio-Collared Adult Elk

The fidelity to summer ranges was 98% by 48 elk that were monitored during 2–5 summers. The two exceptions were a female that summered in Yellowstone National Park in 1980 and 1981 but in Grand Teton National Park in 1982 and a female that summered in the Teton Wilderness in 1978 and 1979 but in the Gros Ventre drainage in 1980.

The fidelity of most animals went beyond returning to one of the four general summer ranges. For example, 10 of the 11 radio-collared elk (monitored ≥ 2 years) that summered in Yellowstone National Park returned to the same drainage or mountain complex each summer.

Yearlings

The percentage of yearlings (sexes combined) among the annual harvests of elk from Grand Teton National Park was significantly higher ($F = 4.4$; 1, 18 df; $P = 0.05$ since 1977; $F = 3.2$; 1, 34 df; $P = 0.08$ since 1969) than the percentage of young during classifications at the National Elk Refuge in previous winters. Since 1969, yearling-male-to-100-female ratios have averaged 21.6 to 100 (SE =

2.3, $n = 20$) in Grand Teton National Park during summer (Table 4) and have been significantly higher than yearling-male-to-100-female ratios on the National Elk Refuge during subsequent winters ($\bar{x} = 10.1 \pm 0.7$, $n = 17$, $t = 4.83$, $P < 0.001$).

Furthermore, an average of 86 ± 2.4 ($n = 18$) elk failed to migrate each spring and remained on the National Elk Refuge in summer. In some years, more than 50% of them were yearling males; 66% (177 of 270) of elk harvested during the first week of the National Elk Refuge hunting seasons since 1978 have been yearling males. New young were not seen on the refuge in summer, and many antlerless elk were yearling females.

We have no data to clarify whether any of these yearlings migrated as 2-year-olds to summer ranges outside Grand Teton National Park. A greater proportion of 3-year-old females than either yearling females ($F = 4.4$; 1, 19 df; $P = 0.05$) or 2-year-old females ($F = 7.7$; 1, 18 df; $P = 0.002$) have been harvested in Grand Teton National Park since 1977.

Spring Migration

Departures of radio-collared elk from the National Elk Refuge in spring peaked approximately 3 weeks after the termination of supplemental feeding, which depended on snowmelt and consequent greening of forage. Males departed

Table 4. Age- and sex-class ratios of elk (*Cervus elaphus*) of the Jackson elk herd on the National Elk Refuge^a, Wyoming, and at the three feed grounds in the Gros Ventre drainage^b, Wyoming, in winter (February) and in the central valley of Grand Teton National Park^c in summer. All counted elk on the National Elk Refuge and at the Gros Ventre drainage feed grounds were classified by age and sex.^d

Year	Winter classifications ^d						Summer classifications ^d						
	National Elk Refuge				Gros Ventre		Grand Teton National Park valley						
	MM:100	YM:100	Y:100	Total	MM:100	Total	MM:100	YM:100	Y:F	Counted	Classified	Estimated	
	F	F	F	elk ^e	F	elk ^e	F	F		elk	elk ^f	total	elk ^g
1969	16.0	10.4	40.2	9,205	2.8	3,224	21	30	30	794	372	1,431	
1970	15.9	9.8	29.4	8,421	2.8	2,334	31	15	32	1,315	586	1,733	
1971	14.2	11.2	30.0	8,054	3.3	2,816	41	24	31	1,037	243	1,131	
1972	15.1	11.1	33.1	7,615	2.5	2,362	48	19	22	765	331	1,611	
1973	15.6	8.8	27.2	7,194	3.8	1,617	14	9	36	899	393	1,644	
1974	13.7	10.6	26.2	7,878	1.9	1,729	64	36	16	1,382	279	1,991	
1975	15.6	10.9	29.7	7,450	3.0	1,366	43	18	38	1,323	615	1,762	
1976	20.7	10.8	34.9	7,858	4.6	1,410	102	18	29	947	399	1,076	
1977 ^h	17.5	13.1	32.6	5,732		NCO ⁱ	165	21	37	1,316	537	1,442	
1978	27.5	7.4	30.0	8,413	6.1	1,703	172	38	47	2,718	636	1,800	
1979	34.6	12.5	33.0	7,828	2.6	1,686	104	18	36	1,512	934	1,667	
1980	37.8	9.9	26.7	7,749	5.1	2,009	200	29	33	1,347	449	1,558	
1981 ^h		NCO ⁱ				NCO ⁱ	182	20	53	1,744	320	1,396	
1982	33.2	10.7	28.0	6,530	2.9	2,095	171	42	49	1,702	398	1,753	
1983	33.8	14.7	29.0	5,878	0.8	1,442				NCO ^j			
1984	37.2	12.0	24.5	5,010	2.2	1,574	310	10	69	1,153	240	1,453	
1985	28.0	8.4	28.0	5,758	1.4	1,328	85	15	39	1,331	599	1,804	
1986	20.3	8.7	30.3	6,430	1.5	1,665	154	17	52	791	791	836 ^k	
1987	19.0	11.6	29.3	7,820	1.5	1,227	54	19	50	1,138	558	1,362	
1988	19.3	12.0	30.8	7,753	2.0	1,567	114	21	71	1,122	336	1,180	
1989	21.0	11.0	34.0	9,486	2.0	2,334	122	18	55	1,871	760	1,909	
Mean	22.8	11.3	30.4	7,403	3.2	1,868	110	22	40	1,192	489	1,527	

^a Data from this study.

^b Wyoming Game and Fish Department, unpublished job completion report.

^c R. P. Wood, unpublished data.

^d F = females > 1-year-old; MM = mature male; YM = yearling male; Y = <1-year-old young of either sex.

^e The number of elk that were classified on feed grounds.

^f The number of the counted elk that were classified.

^g The number of elk that summered in the central valley of Grand Teton National Park based on a Lincoln-Peterson estimator (Martinka 1969).

^h Elk were not supplementally fed during these winters because of limited snow accumulations.

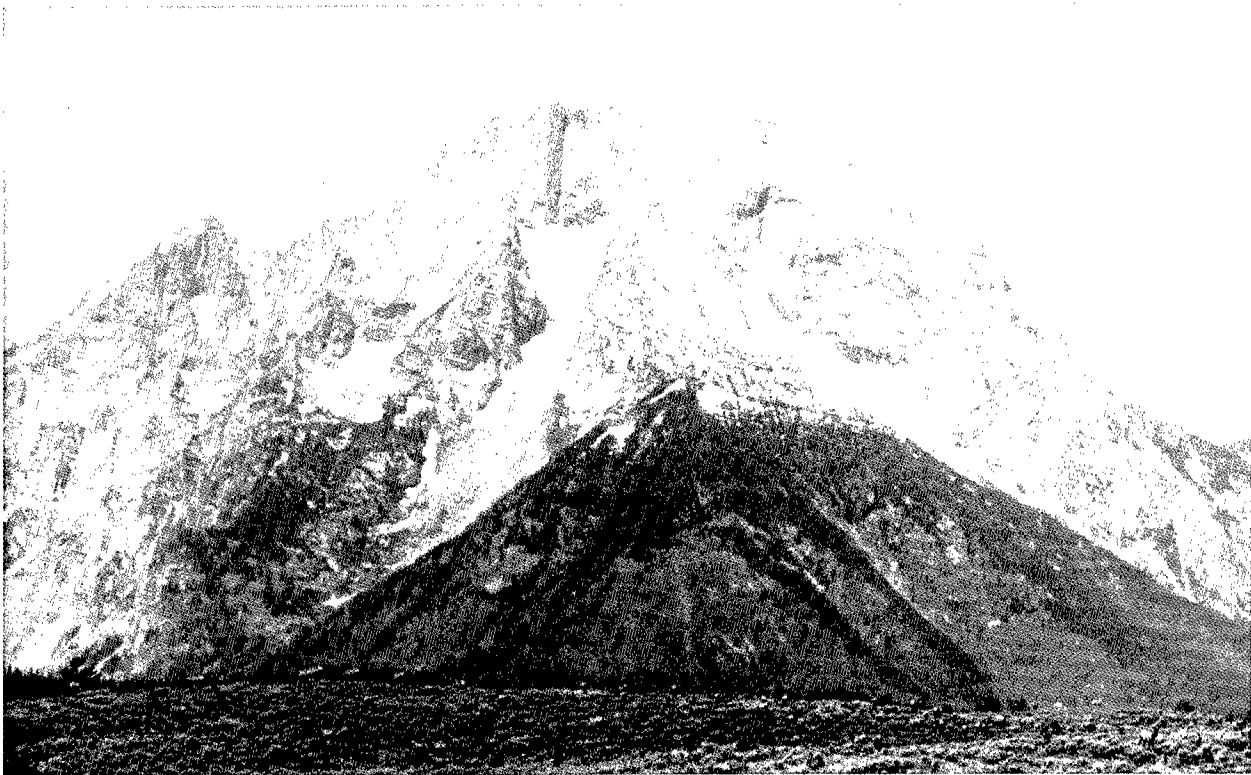
ⁱ NCO = No classification obtained.

^j No count because of adverse weather.

^k A low count was recorded because of fog and poor visibility.



Most elk of the Jackson elk herd migrate from the National Elk Refuge, Wyoming, to their summer ranges in April and May; May 1984.



Elk on the summer range in the central valley of the Grand Teton National Park; July 1985. Mount Moran in the background.

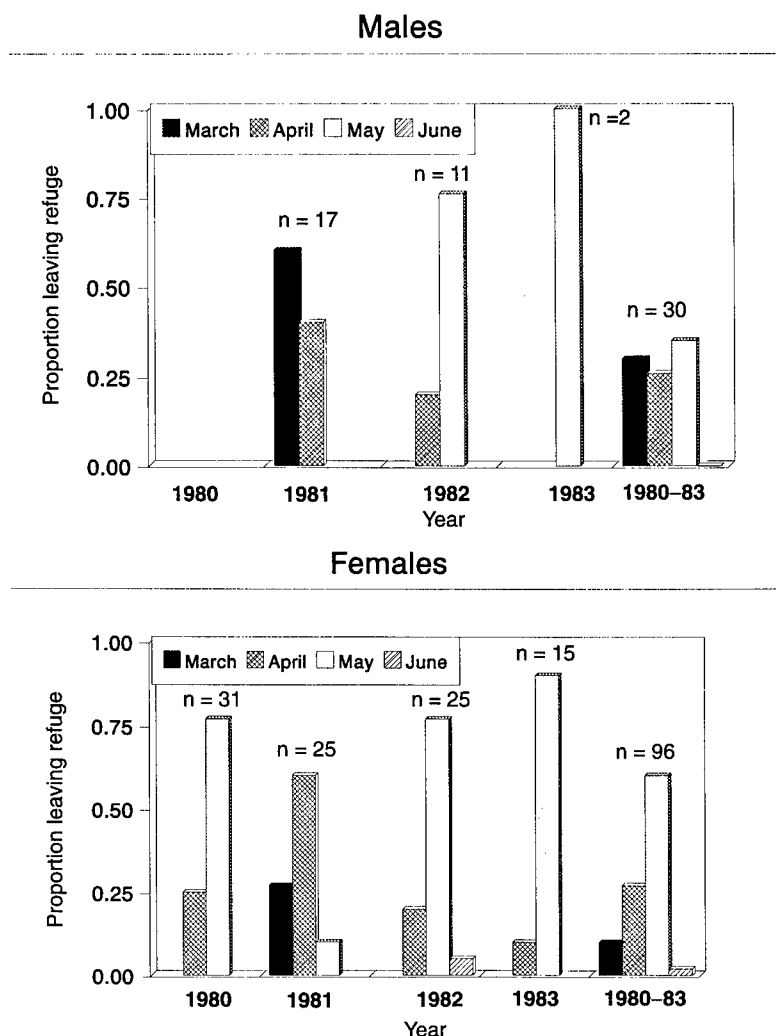


Fig. 4. Spring migration of radio-collared elk from the National Elk Refuge, 1980-1983. Supplemental feeding ended 1 April 1980, 16 April 1982, and 22 April 1983 and was not necessary in 1981.

significantly earlier than females ($X^2 = 15.0$, 3 df, $P < 0.005$; Fig. 4). Elk departed earliest in spring of 1981 when 40% left in March after a winter with low snowfall and no supplemental feeding.

Migrations to summer ranges required only a few days by animals that summered on nearby ranges in Grand Teton National Park or the Gros Ventre drainage. Most female elk that summered in the Teton Wilderness and Yellowstone National Park reached their summer ranges in late June and July. The migrations of most females were interrupted by calving. Male elk arrived at the summer ranges in the Teton Wilderness and Yellowstone National Park 3-4 weeks earlier than female elk.

Fall Migration

The fall migrations commenced in October or November, and 94% of the radio-collared elk arrived at the National Elk Refuge by 15 December (Fig. 5). The durations of fall migrations varied with distances between the summer ranges and the National Elk Refuge (Table 5). The Grand Teton National Park valley and the Gros Ventre drainage herd segments spent significantly less time ($F = 13.8$; 4, 89 df; $P < 0.01$; $\bar{x} = 8.2$ days) in migration than the NW Grand Teton National Park, Teton Wilderness, and Yellowstone National Park herd segments ($\bar{x} = 18.5$ days). Some elk that summered in southern Grand Teton National Park and the

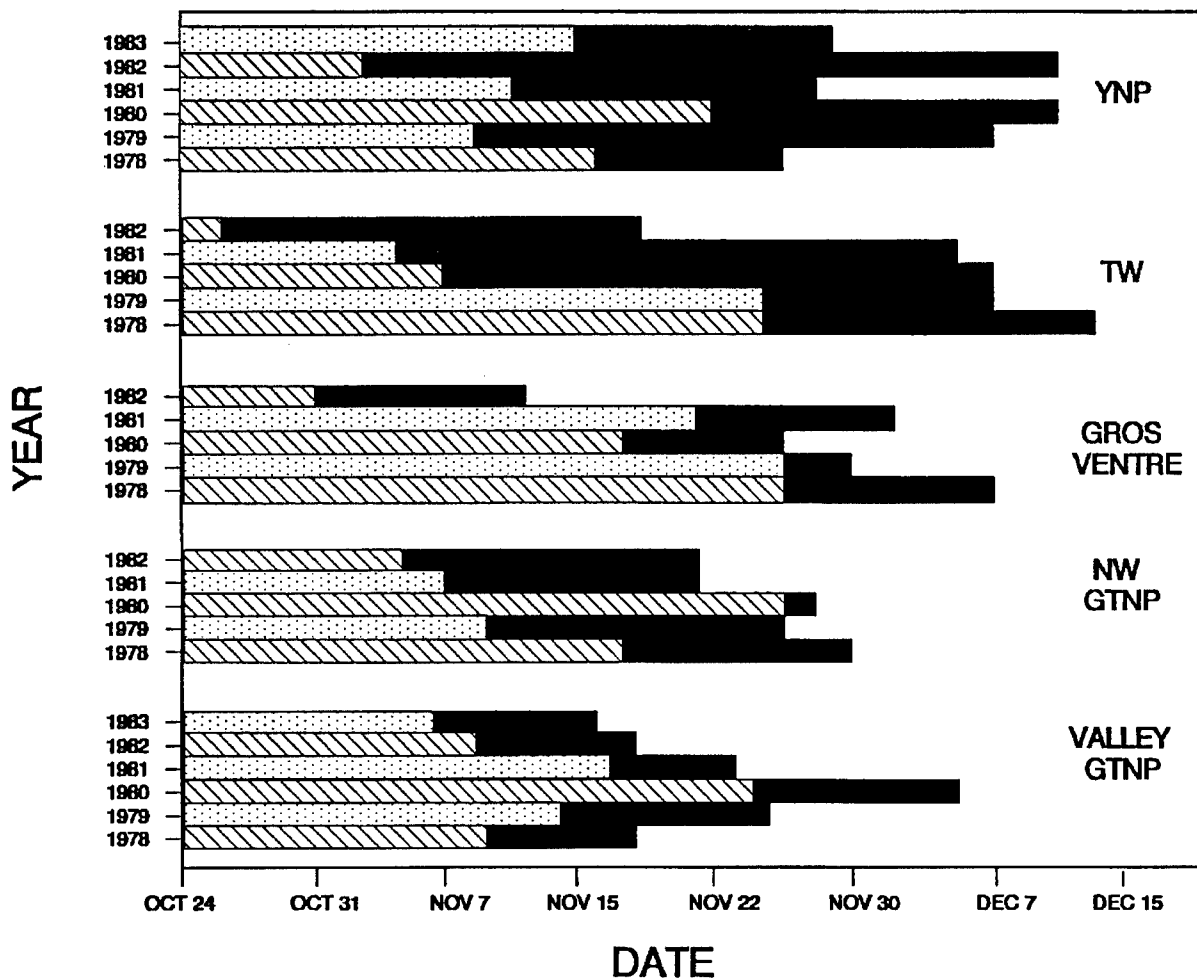


Fig. 5. Mean dates of departure (*left ends of solid bars*) of radio-collared elk from summer ranges in Yellowstone National Park (YNP), Teton Wilderness (TW), Gros Ventre drainage (GV), Northwest Grand Teton National Park (NW GTNP), and Grand Teton National Park (GTNP) valley, and mean dates of arrival (*right ends of solid bars*) at the National Elk Refuge, 1978–83. Lengths of *solid bars* represent the mean annual duration of migration.

western Gros Ventre drainage migrated to the National Elk Refuge in 1 day or less time. Elk that summered in the eastern Gros Ventre drainage, Teton Wilderness, NW Grand Teton National Park (the area west of Jackson Lake), and Yellowstone National Park took from several days to 8 weeks to reach the National Elk Refuge after leaving their summer ranges.

Migration Routes

During fall migrations, the elk funneled southward from their expansive summer ranges to the National Elk Refuge (Fig. 6). Topographic features such as Jackson Lake and steep escarpments con-

centrated elk in places. If heavy snows preceded or coincided with migration, elk took more direct routes and tended to follow drainages and ridgelines.

Migration routes of 5 elk of the Teton Wilderness herd segment (1 male and 4 females) and 15 elk of the Yellowstone National Park herd segment (2 males and 13 females) crossed Grand Teton National Park. Five female elk of the Teton Wilderness herd segment and nine female elk of the Yellowstone National Park herd segment migrated east of Grand Teton National Park. After crossing the Buffalo Fork River, some animals remained east of Grand Teton National Park until they reached the

Table 5. Mean duration of fall migration of radio-collared female elk (*Cervus elaphus*) by herd segment of the Jackson elk herd, 1978–1984. The mean duration of migrations was compared between herd segments with one-way ANOVA and least-significant-difference tests.^a

Herd segment (summer range)	Migration duration			Herd segment (summer range)				
	(days)			Yellowstone	Teton	Gros	Northwest	Grand Teton
	<i>N</i> ^b	$\bar{x}$	SE	National Park	Wilderness	Ventre drainage	Grand Teton National Park	National Park valley
Yellowstone								
National Park	28	20.61	2.18		* ^a	*	*	*
Teton Wilderness	9	25.22	3.88			*	*	*
Gros Ventre drainage	9	9.33	1.89				NSD ^a	NSD
Northwest Grand								
Teton National Park	4	12.25	4.46					*
Grand Teton National								
Park valley	47	7.96	1.08					

^a Asterisk (*) indicates test results were significant at $P < 0.01$; NSD indicates no significant difference.

^b Includes all migrations of elk that were monitored for more than 1 year.

National Elk Refuge, whereas others crossed Grand Teton National Park in Hunting Unit 76 (Fig. 3).

Arrival at the National Elk Refuge

The mean annual arrival dates of radio-collared elk highly correlated with the arrival of the entire Jackson elk herd at the National Elk Refuge ($r = 0.946$, 6 df, $P < 0.01$; Fig. 7). Radio-collared elk that summered in Grand Teton National Park arrived significantly earlier (i.e., 6–15 days; $F = 16.9$; 3, 137 df; $P < 0.005$) at the National Elk Refuge than elk from the other summer ranges (Table 6). Radio-collared elk from the Grand Teton National Park valley (all areas except northwestern Grand Teton National Park) arrived earlier ($t = 2.31$, 86 df, $P < 0.05$) at the National Elk Refuge than elk that summered in northwestern Grand Teton National Park.

A significantly greater proportion of male (0.72) and female (0.49) elk that summered in Grand Teton National Park than males (0.29) and females (0.13) that summered outside Grand Teton National Park arrived at the National Elk Refuge before 23 November (males: $Z = 2.00$, $P = 0.023$; females: $Z = 4.07$, $P < 0.001$). Through 30 November, 80% of the elk that arrived at the National Elk Refuge were from Grand Teton National Park (Table 7).

Of the Grand Teton National Park herd segment, males arrived earlier at the National Elk Refuge than females ($Z = 1.79$, $P = 0.04$). The mean arrival

dates of elk from the other herd segments did not differ by sex ($Z = 1.13$, $P = 0.13$; Table 7).

Timing of Fall Migrations

The mean annual departure dates of radio-collared elk from their summer ranges during 1978–83 inversely correlated with October precipitation at Moose, Wyoming ($r = -0.79$, 5 df, $P = 0.06$). Including mean October temperatures as a second independent variable did not increase the predictability of departure dates ($r = 0.77$, 5 df, $P = 0.22$). Although the elk departed from their summer ranges earlier in years when precipitation was greater, they did not arrive significantly earlier at the National Elk Refuge ($r = -0.69$, 5 df, $P = 0.13$). However, the later elk departed from the more distant summer ranges in Yellowstone National Park, in the Teton Wilderness, and in northwestern Grand Teton National Park, the fewer days they spent migrating to the National Elk Refuge ($r = 0.41$, 5 df, $P < 0.01$; Fig. 5).

The arrival of radio-collared females from the Teton Wilderness and Yellowstone National Park herd segments at the refuge inversely correlated with snow depths on 30 November at Moose, Wyoming ($r = -0.762$, 6 df, $P < 0.05$), and at Moran, Wyoming, ($r = -0.832$, 6 df, $P < 0.05$). Correlations increased when radio-collared males were included in the analyses (Moose: $r = -0.949$, 6 df, $P < 0.01$; Moran: $r = -0.946$, 6 df, $P < 0.01$). Likewise,

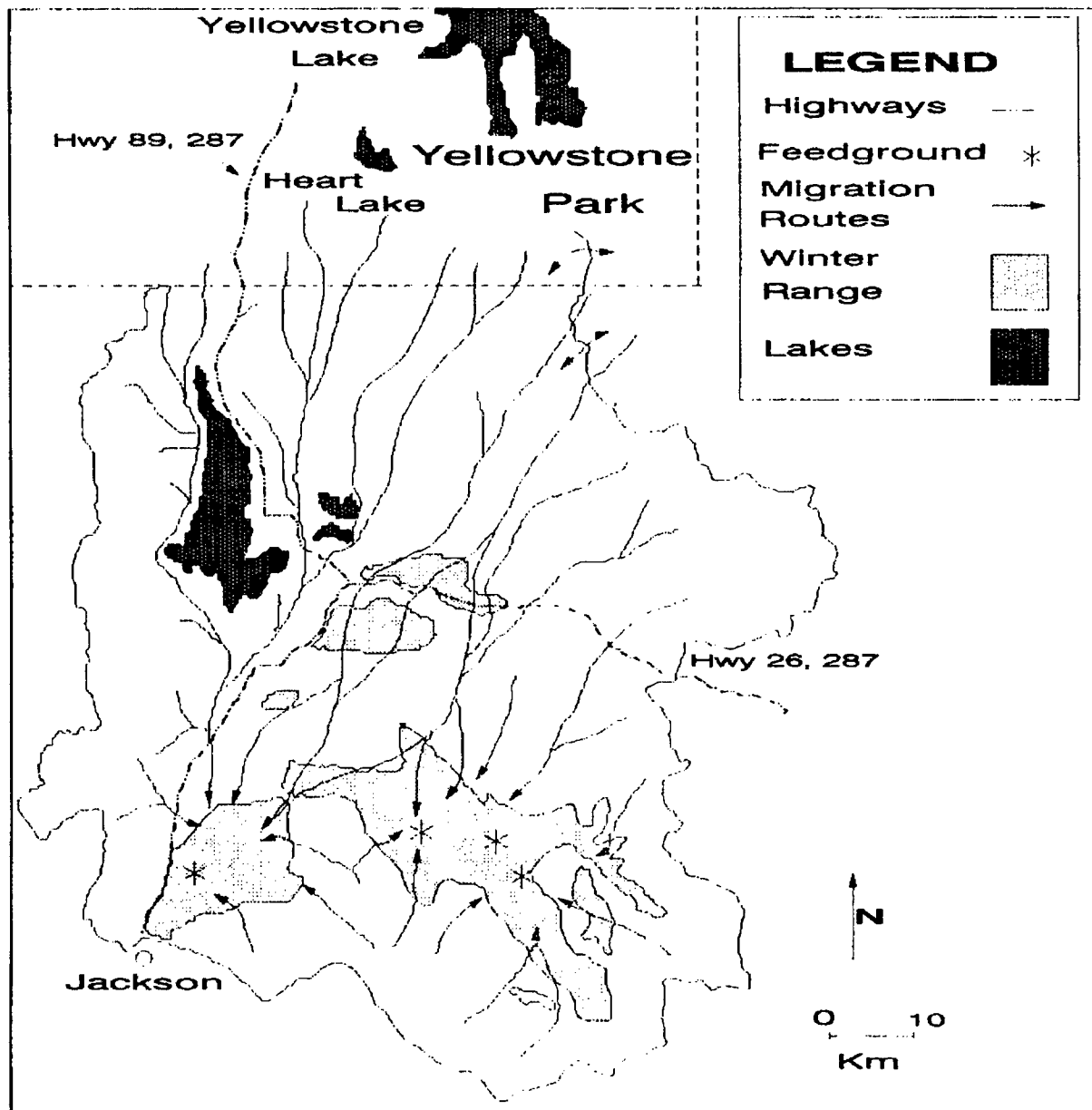


Fig. 6. Migration routes in the Jackson herd unit (adapted from Boyce 1989).

the mean arrival dates of all elk at the refuge (based on dates when 50% of the wintering population reached the National Elk Refuge) correlated with snow depths on 30 November during 1969–85 (Moose: $r = -0.790$, 16 df, $P < 0.01$; Moran: $r = -0.786$, 16 df, $P < 0.01$). The arrivals of radio-collared elk of the Grand Teton National Park and Gros Ventre Drainage herd segments at the Na-

tional Elk Refuge did not correlate with snow depths at Moose (Grand Teton National Park: $r = -0.412$, 6 df, $P > 0.10$; Gros Ventre drainage: $r = 0.299$, 6 df, $P > 0.10$) and Moran (Grand Teton National Park: $r = -0.680$, 6 df, $P > 0.05$; Gros Ventre drainage: $r = 0.298$, 6 df, $P > 0.10$). Snowfall accumulations and annual precipitation increase from south to north in the study area (i.e., from

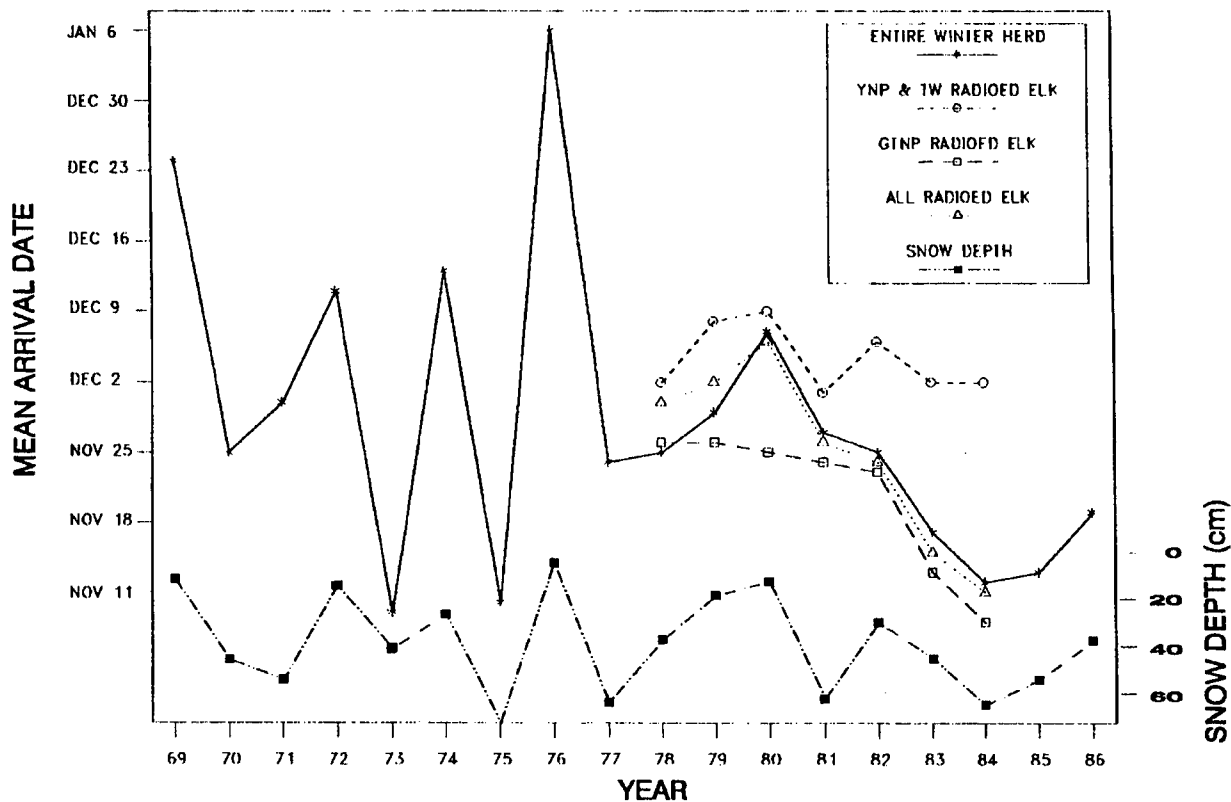


Fig. 7. Relation of 30-November snow depths at Moran, Wyoming, to mean arrival dates of radio-collared elk of the Grand Teton National Park (GTNP), Yellowstone National Park (YNP) and Teton Wilderness (TW) herd segments and all radio-collared elk (*Cervus elaphus*), and mean arrival dates of 50% of the total number of elk that wintered at the National Elk Refuge, 1969–1986.

Table 6. Mean 1978–1984 arrival dates at the National Elk Refuge, Wyoming, of radio-collared female elk (*Cervus elaphus*) of the Jackson elk herd returning from summer ranges. Data are presented by herd segment, each of which is identified by its summer range. One-way ANOVA and pairwise least-significant-difference tests were used to compare dates between herd segments.^a

Herd segment (summer range)	N ^b	Mean arrival dates		Summer range			
		Calendar	Julian (SE)	Yellowstone National Park	Teton Wilderness	Gros Ventre drainage	Grand Teton National Park
Yellowstone National Park	33	5 Dec.	339.2 (9.41)		NSD ^a	* ^a	*
Teton Wilderness	10	6 Dec.	340.4 (7.51)			*	*
Gros Ventre drainage	12	27 Nov.	331.0 (13.11)				*
Grand Teton National Park	88	21 Nov.	325.1 (11.78)				

^a Asterisk (*) indicates test results were significant at $P < 0.05$; NSD indicates no significant difference.

^b Includes all migrations of elk that were monitored for more than 1 year.

Table 7. Dates of arrival of radio-collared elk (*Cervus elaphus*) on the National Elk Refuge, Wyoming, on return from summer ranges, 1978–1983. Data are presented by herd segment, each of which is identified by its summer range.

Herd segment (summer range)	Sex	N ^b	Number (%) of elk ^a arriving before					
			November			December		January
			1	16	23	1	16	1
Yellowstone National Park	female	30	0	1	3(10)	9(30)	24(80)	29(97)
	male	3	0	0	0	1	2	
Teton Wilderness	female	9	0	0	1(11)	2(22)	8(89)	9(100)
	male	2	1 ^c	1 ^c	1 ^c	1 ^c	2	0
Gros Ventre drainage	female	9	0	1	2(22)	3(33)	9(100)	0
	male	2	0	1	1	2	0	0
Northwest Grand Teton National Park	female	6	0	0	0	4	6	0
	male	3	0	0	2	3	0	0
Grand Teton National Park valley	female	64	1	18	34(53)	52(81)	63(98)	0
	male	15	1	7	11(73)	15(100)	0	0
Yellowstone National Park, Teton Wilderness, and Gros Ventre drainage	female	48	0	2	6(12)	14(29)	41(85)	47(98)
	male	7	1 ^c	2	2	4	7(100)	0
All Grand Teton National Park	female	70	1	18	34(49)	56(80)	69(99)	69(99)
	male	18	1	7	13(72)	18(100)	0	0

^aData include elk harvested in Hunting Unit 76 of Grand Teton National Park and Hunting Unit 77 of the National Elk Refuge.

^bIncludes all migrations of elk that were monitored for more than 1 year.

^cThis elk was in poor condition and died of natural causes within 2 weeks of its arrival at the National Elk Refuge.

Jackson to Moose to Moran, Wyoming, to the south entrance of Yellowstone National Park; $r = 0.96$, $df = 3$, $P < 0.01$, and $r = 0.99$, $df = 3$, $P < 0.01$). Therefore, Grand Teton National Park and the Gros Ventre drainage receive less snowfall during October and November than Yellowstone National Park and the Teton Wilderness. Likewise, there is a gradient in mean annual temperature from Jackson, Wyoming, to Yellowstone National Park ($r = -0.98$, $df = 3$, $P < 0.01$). Inclusion of the mean monthly October or mean monthly November temperatures as a second independent variable did not improve the predictability of any models.

Duration of Migrations

The mean annual dates of departure from the summer ranges did not differ between elk that summered in Grand Teton National Park and elk that summered on ranges outside Grand Teton National Park ($t = 0.115$, 10 df , $P > 0.5$) and not between elk that summered in Grand Teton National Park valley and elk from all other summer ranges ($t = 0.093$, 10 df , $P > 0.5$). Thus, the longer duration of the fall migration (time between de-

parture from the summer range and arrival at the National Elk Refuge) accounted for the later arrival of elk that summered outside Grand Teton National Park ($F = 8.88$; 1, 12 df ; $P < 0.025$). Elk that summered in the Grand Teton National Park valley spent much of the time between their departure from summer range and arrival at the National Elk Refuge staging on the Baseline Flat in Grand Teton National Park (Fig. 1). Prior to crossing the Snake River and completing the migration to the National Elk Refuge, hundreds to several thousands of elk gathered and foraged each November on sagebrush-grasslands west of the Snake River. During fall of 1982 and 1983 when they were consistently relocated every 3 days, the elk that summered in the Grand Teton National Park valley spent 77% of their migration time staging on the Baseline Flat ($\bar{x}$ migration time = 10.7 days, $\bar{x}$ staging time = 8.2 days, $n = 26$). If their summer ranges included the Baseline Flat, the elk were excluded from the analysis. Some elk of the NW Grand Teton National Park, Teton Wilderness, and Yellowstone National Park herd segments, which migrated to the National Elk Refuge through Grand Teton National Park,

also staged on the Baseline Flat. An insufficient number of radio relocations precluded a comparison by herd segment of the lengths of time elk spent staging.

Calving

Calving Locations

Sixty-five female elk were monitored during 131 calving opportunities (1–4 calving seasons each). We collected 449 relocations of those females during the peak parturition period (25 May–15 June) from 1978 to 1983. The 18 relocations not shown on Figure 8 were scattered along the east side of Jackson Lake, in the Teton Wilderness, and in southern areas of Grand Teton National Park.

During the study, we confirmed calving by 9 different radio-collared females. Relocations of those animals (7 summered in Grand Teton National Park and 2 in Yellowstone National Park) were typical of the general pattern of relocations of all radio-collared female elk from 25 May to 15 June (Fig. 8).

Delineation of Calving Areas

The 65 radio-collared female elk frequented only 8% of the 5,195 1-km² grid squares in the Jackson herd unit during the peak parturition period. The 65 were a fraction of the total number of calving females in the Jackson herd unit. We delineated seven calving areas from the clumped distribution of relocations (Fig. 8). Most relocations (342) were concentrated in the Grand Teton National Park valley calving area between the Moose townsite and Two Ocean Lake (Fig. 8). In addition to the calving area in Grand Teton National Park valley, 6 other calving areas were identified at (1) the Snake River in Yellowstone National Park, (2) North Jackson Lake, (3) Pacific Creek, (4) Mt. Randolph, (5) Slate Creek, and (6) the South Gros Ventre drainage (Fig. 8). Whereas elk from all herd segments used the Grand Teton National Park valley calving area, only elk of the Yellowstone National Park herd segment used the Snake River calving area, only elk of the Yellowstone National Park and NW Grand Teton National Park herd segments used the North Jackson Lake calving area, only elk of the Yellowstone

National Park and Teton Wilderness herd segments used the Pacific Creek and Mt. Randolph calving areas, and only elk of the Gros Ventre Drainage segment used the Slate Creek and South Gros Ventre calving areas (Table 8).

Radio-collared elk calved in 12 cattle grazing allotments and in the summer range of the Jackson bison herd (Figs. 8–10). In five cattle allotments, the grazing season began during the 25 May–15 June peak of elk parturition. These include the Spread Creek-Uhl Hill cattle allotment in Grand Teton National Park, the Fish Creek and Blackrock-Spread Creek allotments in the Bridger-Teton National Forest, and the Pacific Creek allotments in Grand Teton National Park and the Bridger-Teton National Forest (Appendix D). Although the start of grazing in the Blackrock-Spread Creek allotment was scheduled for 15 June, cattle from the Spread Creek-Uhl Hill allotment often grazed in this important elk-calving area earlier in June.

We did not sample characteristics of sites where we relocated elk. In general, elevations between 2,000 and 2,500 m, warm aspects (S, SW, or SE) with gentle slopes, and plant communities of sagebrush-grassland and aspen mixed with coniferous forests or—in some areas—willow shrublands were typical of the calving areas.

Affinities by Herd Segment

Ninety-one (69%) of 131 opportunities for calving occurred in the Grand Teton National Park valley and included elk from every herd segment (Table 8). In another 17 (13%) calving opportunities, elk frequented the valley and one other calving area. Thus, as many as 82% of the young of radio-collared elk may have been born in the Grand Teton National Park valley. Sixty-three (58%) of those 108 calving opportunities were attributable to elk that summered in the Grand Teton National Park valley. All radio-collared females that summered in the Grand Teton National Park valley were relocated in only the Grand Teton National Park valley calving area during 25 May–15 June.

Elk from the Yellowstone National Park, Teton Wilderness, and Gros Ventre Drainage herd segments used 3–5 of the 7 calving areas (Table 8). Elk of the Yellowstone National Park herd segment used all calving areas that their migra-

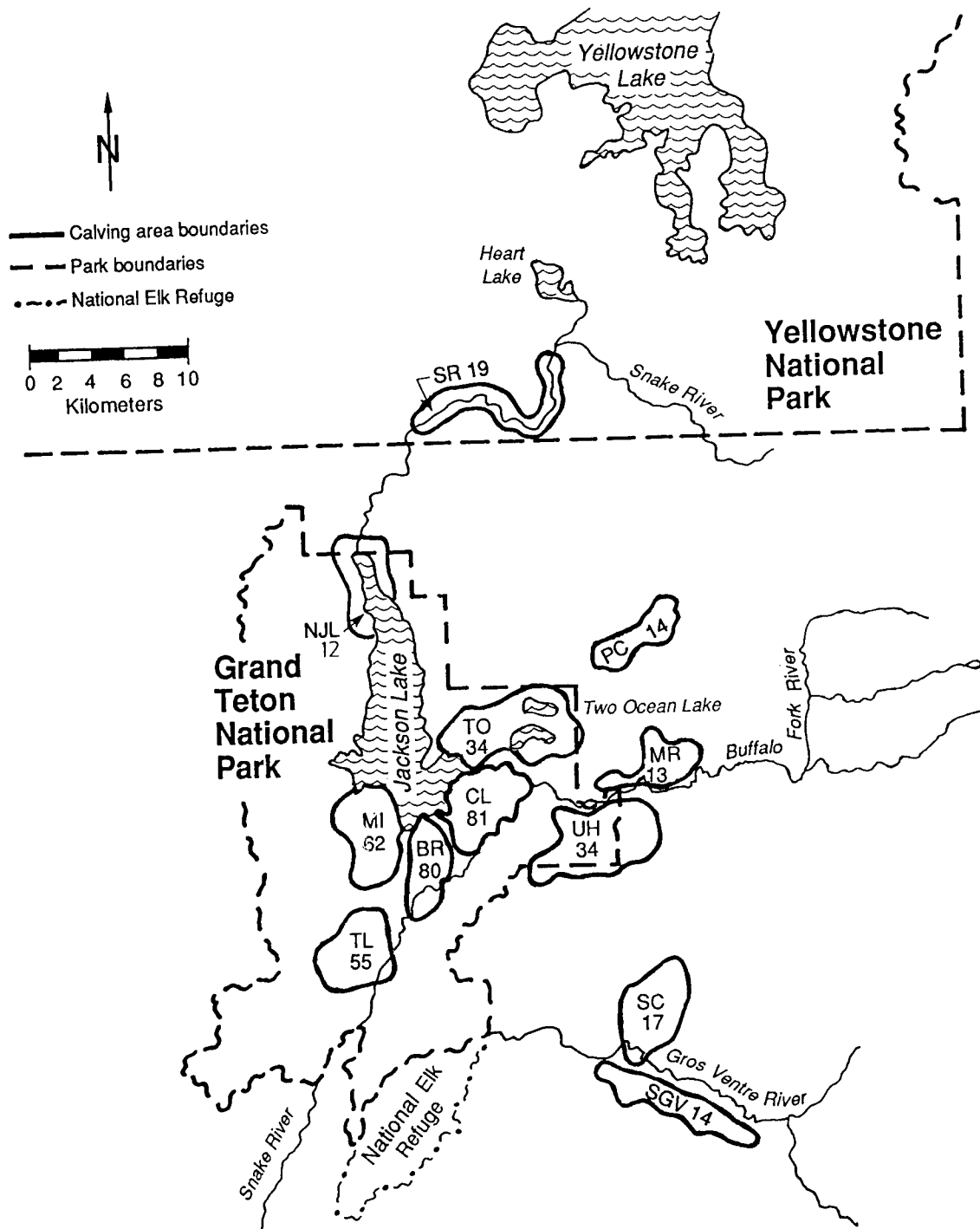


Fig. 8. Number of relocations of radio-collared female elk during the peak parturition period of 25 May–15 June 1978–1983 in each calving area: Snake River (SR), North Jackson Lake (NJL), Pacific Creek (PC), Mount Randolph (MR), Slate Creek (SC), and South Gros Ventre (SGV). The Grand Teton National Park valley calving area is subdivided into six calving centers: Two Ocean Lake (TO), Spread Creek-Uhl Hill (UH), Cow Lake-Signal Mountain (CL), Burned Ridge-Potholes (BR), Mystic Isle Burn (MI), and Taggart Lake-Baseline Flat (TL).

Table 8. Number of radio-collared elk (*Cervus elaphus*) of the Jackson elk herd that used the calving areas in the Grand Teton National Park valley, northwest Grand Teton National Park, Yellowstone National Park, Teton Wilderness, and the Gros Ventre drainage from 25 May to 15 June 1978–1983. Data represent the number of radio-collared elk that used each calving area summed across all 6 years and are presented by herd segment, each of which is identified by its summer range.

Calving areas	Herd segments (summer range)					Total
	Grand Teton National Park valley	Northwest Grand Teton National Park	Yellowstone National Park	Teton Wilderness	Gros Ventre	
Grand Teton National Park valley	63	3	14	6	5	91
Snake River in Yellowstone National Park ^a	0	0	10	0	0	10
North Jackson Lake ^a	0	1	4	0	0	5
Pacific Creek ^a	0	0	5	2	0	7
Mount Randolph ^a	0	0	3	2	0	5
Slate Creek	0	0	0	0	5	5
South Gros Ventre	0	0	0	0	5	5
Snake River and North Jackson Lake	0	0	1	0	0	1
North Fork Buffalo River	0	0	0	2	0	2
Total	63	4	37	12	15	131

^a Some relocations of elk in these calving areas were also made in the Grand Teton National Park valley. No elk used more than 2 areas/year.

tion routes crossed (Valley, Pacific Creek, Mount Randolph, North Jackson Lake, and Snake River in Yellowstone National Park calving areas), and elk of the Teton Wilderness used all calving areas that their migrations routes crossed (Valley, Pacific Creek, and Mount Randolph calving areas).

Five of 15 elk of the Gros Ventre drainage herd segment spent the calving season in the Pot-holes, Signal Mountain, or Spread Creek of the Grand Teton National Park valley before migrating southeast to their summer ranges (Figs. 2 and 8).

Fidelity to Calving Areas

The fidelity to calving areas was 78% (50 of 64 opportunities) among the radio-collared female elk that were monitored during two or more successive calving seasons (Table 9). The fidelity to calving areas was 100% by the female elk that summered in the Grand Teton National Park valley but 55% by the female elk that summered elsewhere. The elk of the Yellowstone National Park herd segment were least loyal. They changed calving areas 67% of the time in sub-

sequent years and more than the elk of NW Grand Teton National Park (50%), Teton Wilderness (43%), and Gros Ventre drainage (0%) herd segments. Fidelity inversely correlated with distance between the winter range and each calving area ($r = -0.83$, 6 df, $P < 0.05$).

More female elk of the Yellowstone National Park herd segment used the Snake River calving area (the highest in elevation and farthest from the National Elk Refuge) in 1981 than in other years of the study. During this study, the snowpack melted and vegetation began greening earliest in spring of 1981. Of three elk of the Yellowstone National Park herd segment that spent the 1981 calving period at the Snake River calving area, only one calved there the previous year. Of five elk of the Yellowstone National Park herd segment that were monitored during the 1981 calving season, two returned to the Grand Teton National Park valley calving area and one returned to the Snake River calving area in 1982. The other two female elk spent the 1981 calving season at the Snake River calving area but used the more southern Grand Teton National Park valley and

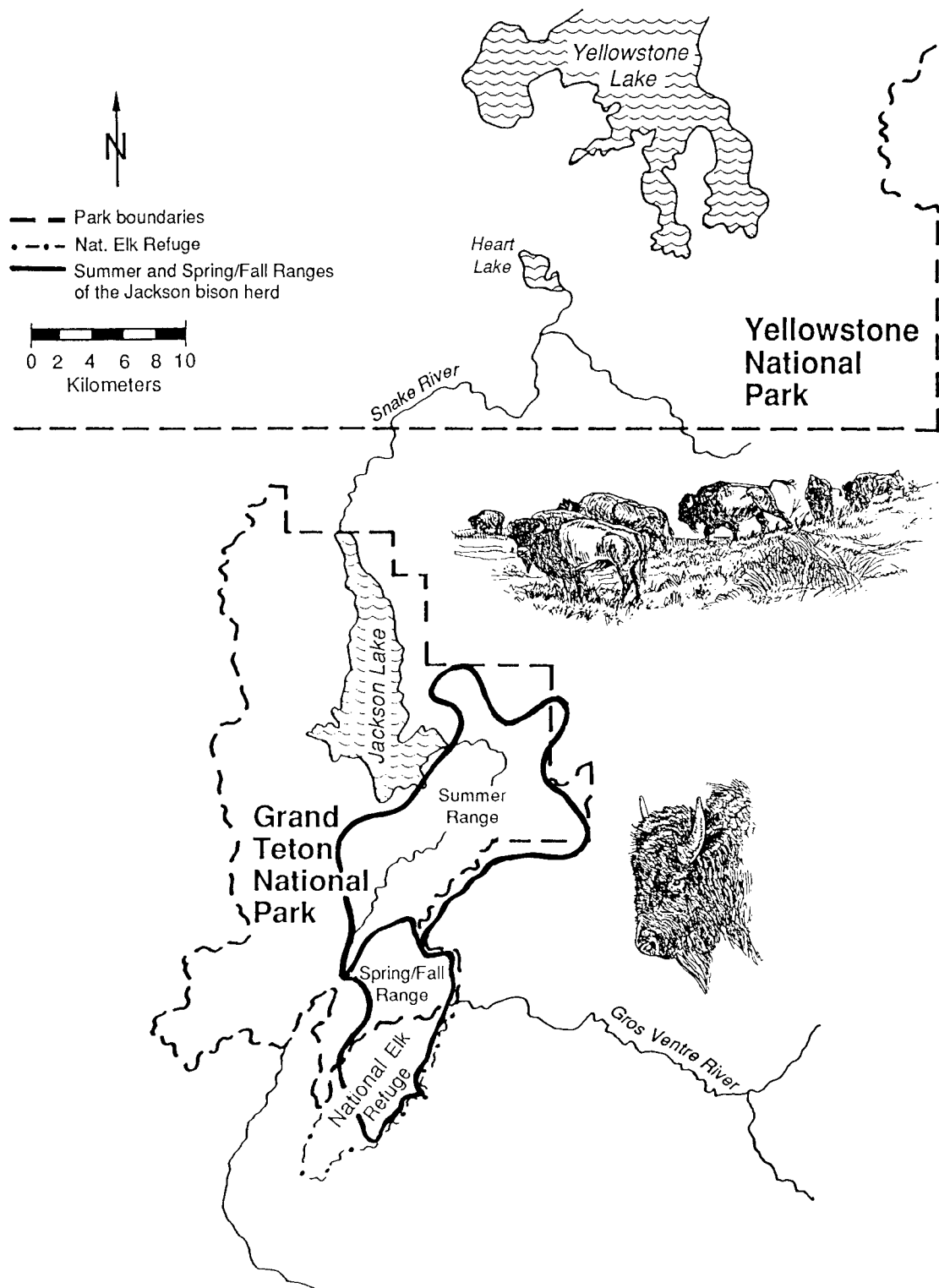


Fig. 9. Summer and spring-fall ranges of the Jackson bison herd.

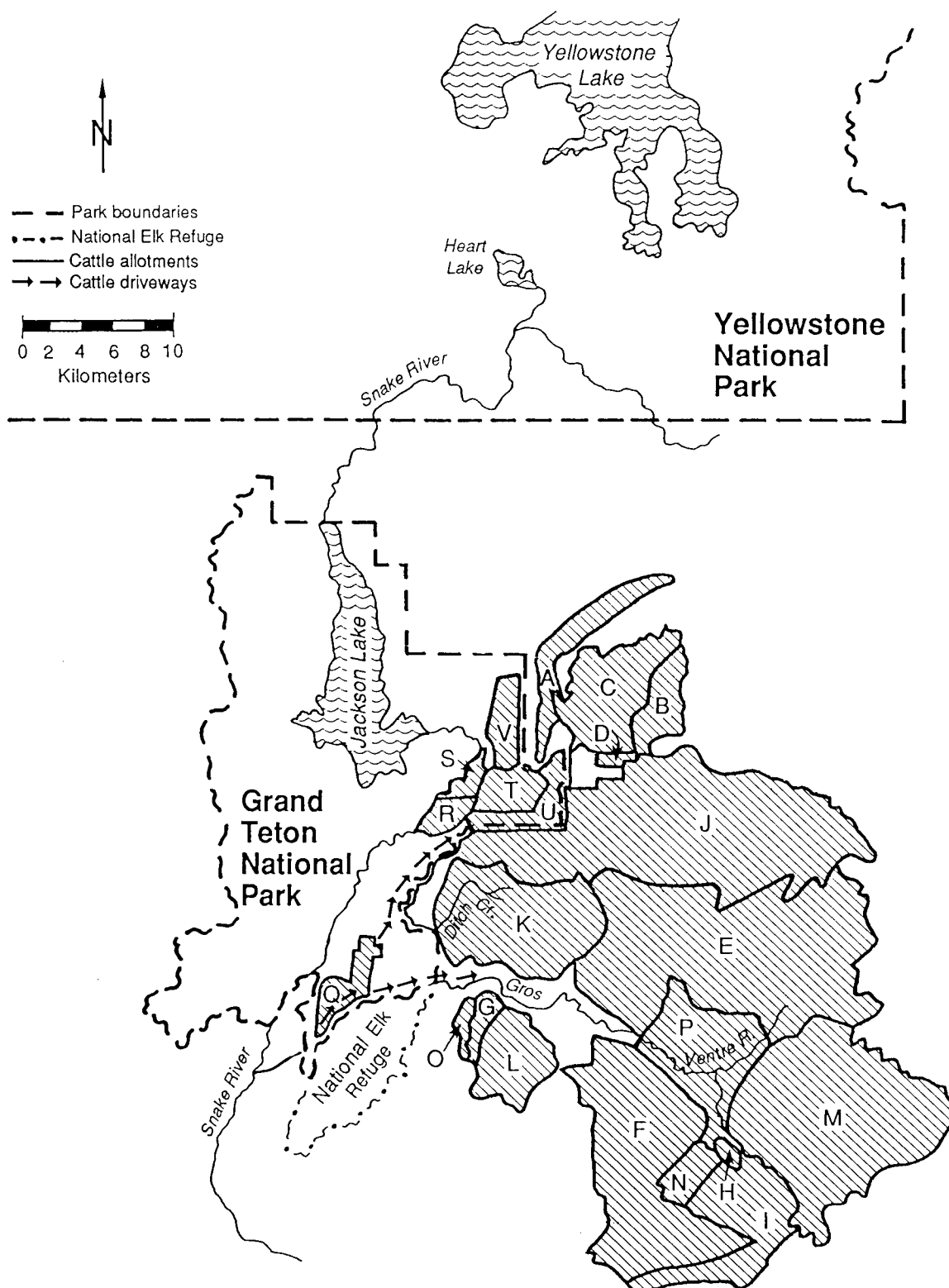


Fig. 10. Cattle allotments (*capital letters*) and cattle driveways (*arrows*) in the Jackson elk herd unit. Appendix D lists grazing dates and stocking rates of each allotment.

Table 9. Fidelity to calving areas (based on the area in which most relocations were made from 25 May to 15 June) by radio-collared female elk (*Cervus elaphus*) of the Jackson elk herd, Wyoming. Only elk monitored during 2 or more successive calving seasons are included.

Calving area in year X	Calving area in year X + 1								Total
	Grand Teton valley	Snake River	North Jackson Lake	Pacific Creek	Mount Randolph	Slate Creek	South Gros Ventre	North Fork Buffalo	
Grand Teton valley	40	2	1	2	2	0	0	0	47
Snake River	1	2	1	0	0	0	0	0	4
North Jackson Lake	1	1	0	0	0	0	0	0	2
Pacific Creek	1	1	0	0	0	0	0	0	2
Mount Randolph	1	0	0	0	1	0	0	0	2
Slate Creek	0	0	0	0	0	3	0	0	3
South Gros Ventre	0	0	0	0	0	0	3	0	3
North Fork Buffalo	0	0	0	0	0	0	0	1	1
Total	44	6	2	2	3	3	3	1	64

North Jackson Lake calving areas in 1982. Spring arrived late in 1982 and supplemental feeding on the National Elk Refuge continued until 16 April (Fig. 4).

Fidelity was best predicted by a multiple regression of three independent variables: elevation of the calving area, distance of the calving area from the National Elk Refuge, and mean annual temperature ($R^2 = 0.99$, 4 df, $P = 0.04$). Mean annual precipitation and snowfall did not significantly contribute to any regression equations.

Grand Teton National Park Valley Calving Area

The most intensively used calving area was the Grand Teton National Park valley. Relocations there were clustered in six calving centers, ranging from 9 to 16 km² (Fig. 8). Distributions of 28 elk that spent the calving season in the Grand Teton National Park valley were restricted to 1 of these 6 calving centers during any year. The remaining 33 (54%) elk travelled between two or three centers (based on female elk that were relocated at least once each week during the 3-week calving period). The percentage of animals that used more than one calving center in the valley did not differ ($Z = -0.18$, $P = 0.43$) between elk that summered in the Grand Teton National Park

valley (53%) and elk that summered in all other locations (56%).

Female elk that summered in the Grand Teton National Park valley used the southern and western calving centers most. Female elk from the Yellowstone National Park and Gros Ventre herd segments frequented the northern and eastern calving centers most. Elk that summered in northwest Grand Teton National Park, which migrate along the west side of Jackson Lake to reach their summer ranges, were found in only the Mystic Isle Burn and Burned Ridge-Potholes calving centers (Table 10).

Natality

Pregnancy rates were 17% of 50 1.5-year-old female elk and 87% of 318 ≥ 2.5 -year-old female elk that were trapped on the National Elk Refuge during 1976–82. The expected natality was 68 young/100 female elk (Figure 11). Reducing this estimate by 7% to account for losses of fetuses from brucellosis (Oldemeyer et al. 1993), we expected 63 young/100 female elk at birth.

Since 1970, midwinter young-to-100-female-elk ratios at the National Elk Refuge have averaged 29.6 ± 2.9 or about 50% of the expected ratios (Table 4). Over half of the difference between the expected and observed production was lost by

Table 10. Use of calving centers in the Grand Teton valley calving area by radio-collared female elk (*Cervus elaphus*) of the Jackson elk herd, Wyoming, during 25 May–15 June 1978–1983. Telemetric relocations of the elk are presented by herd segment, each of which is identified by its summer range and expressed in relative frequency of use.

Herd segment (summer range)	Taggart Lake– Baseline Flat	Mystic Isle Burn	Burned Ridge and Potholes	Cow Lake– Signal Mountain	Spread Creek– Uhl Hill	Two Ocean Lake	Total
Grand Teton							
National Park valley	47	50	67	44	3	9	220
Northwest Grand							
Teton National Park	0	11	4	0	0	0	15
Yellowstone National							
Park	0	1	6	24	26	24	81
Teton Wilderness	8	0	1	4	2	0	15
Gros Ventre drainage	0	0	2	9	3	1	15
Total	55	62	80	81	34	34	342

midsummer when the young-to-female-elk ratios had declined to about 45:100 throughout the Jackson herd unit (Table 11). The additional decline ($F = 13.8$; 1, 8 df; $P = 0.006$) in the young-to-female-elk ratios on the National Elk Refuge from midsummers 1978–83 to the following winters could not be explained by hunter selection of young. Only 30.1

young:100 female elk were harvested during falls 1978–83 (30.3:100 during 1969–86; Boyce 1989, Appendix C). Either the mortality of young (not attributable to hunter selectivity for young) occurred between midsummer and midwinter or the midsummer young-to-female-elk classifications are biased upward.

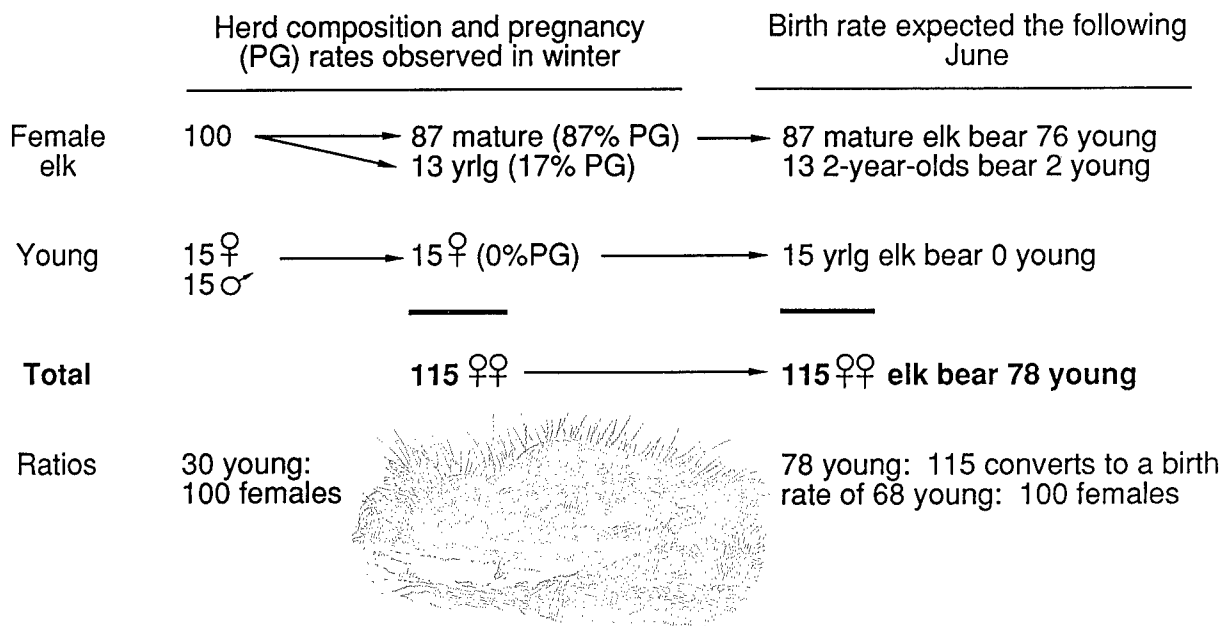


Fig. 11. Expected and observed ratios of young (<1 year old) female (>1 year old) elk (*Cervus elaphus*) of the Jackson elk herd, Wyoming. The winter herd composition since 1970 ($n = 15$) and the pregnancy rates of yearlings (yrlg) and mature females during winters of 1976–78 were collected at the National Elk Refuge, Wyoming.

Table 11. Young-to-female (> 1-year-old) ratios of the herd segments of the Jackson elk (*Cervus elaphus*) herd, 1978–1983. Herd segments are identified by their summer ranges.

Herd segment (summer range)	Year						Total
	1978	1979	1980	1981	1982	1983	
Grand Teton National Park							
Young	259	220	411				890
Females	592	544	838				1,974
Ratio	44:100	40:100	49:100				44.4:100
Teton Wilderness							
Young			89			27	116
Females			179			82	261
Ratio			50:100			33:100	41.3:100
Yellowstone National Park							
Young	63	243	47		116		469
Females	124	559	117		310		1,110
Ratio	51:100	43:100	40:100		37:100		43.0:100
Gros Ventre drainage^a							
Young	190	268					458
Females	407	457					864
Ratio	47:100	59:100					53.0:100

^aData from G. Roby, Wyoming Game and Fish Department.

Ratios did not differ by herd segment ($F_{3,10} = 1.11$; $P = 0.4$).

Young-to-female ratios that we observed in Grand Teton National Park ($\bar{x} = 44.4:100$) did not differ ($t = 0.018$, 8 df, $P = 0.9$) from ratios recorded by personnel of Grand Teton National Park during 1978–83 ($\bar{x} = 43.6:100$; Table 4).

Harvests

Harvest Rates of Radio-collared Elk

During 1978–84, 35 of the 85 radio-collared elk were harvested. Because some animals were monitored for two or more hunting seasons, there were 175 opportunities for the 85 elk to be harvested. The mean annual harvest rate was 20.0% (Table 12). The elk that summered in the national parks were harvested at lower rates (25 of 143 = 17.5%) than the elk that summered in the national forest (10 of 32 = 24.3%; $Z = -1.76$, $P = 0.04$). Elk from the Gros Ventre herd segment were harvested at the highest rates, and elk from the Grand Teton National Park herd segment were harvested at the lowest rates (Table 12).

Harvest of Radio-collared Elk by Sex

Males of the Grand Teton National Park herd segment (11.1%) and females of the Yellowstone

National Park herd segment (15.8%) were harvested at the lowest rates (Table 12). Harvest rates differed ($X^2 = 5.2$, 1 df, $P = 0.02$) between the sexes of elk that summered outside (male = 50.0%; female = 20.3%) Grand Teton National Park. Harvest rates did not differ between the sexes of elk inside Grand Teton National Park ($X^2 = 0.5$, 1 df, $P = 0.47$, male = 11.1%; female = 18.0%) and not between all radio-collared males (25.0%) and females (19.0%; $X^2 = 1.1$, 1 df, $P = 0.29$; Table 12; probably because of the small sample sizes). Harvest rates of males ($X^2 = 5.2$, 1 df, $P = 0.02$) but not of females ($X^2 = 0.1$, 1 df, $P = 0.73$) were significantly higher outside Grand Teton National Park, where the hunting of either-sex elk was the rule, than inside Grand Teton National Park.

Harvests in the Jackson Herd Unit, 1978–1983

The lower harvest rate of radio-collared male elk in Grand Teton National Park than outside Grand Teton National Park occurred during years

Table 12. Number of radio-collared elk (*Cervus elaphus*) of the Jackson elk herd that were harvested during 1978–1983. Data are presented by herd segment, each of which is identified by its summer range. Harvests of radio-collared elk in Hunting Units 75,76, and 79 of Grand Teton National Park and in Hunting Unit 77 on the National Elk Refuge, Wyoming, are shown by week.

Herd segment by sex	Number ^a	Harvested in Grand Teton National Park and on the National Elk Refuge						
		Harvested Number	(%)	Before 11/16	11/16– 11/23	11/24– 11/30	After 11/30	Hunting season
Grand Teton National Park								
Male	18	2	(11.1)	1	1	0	0	2
Female	83	15	(18.1)	1	5	6	3	15
Both	101	17	(16.8)	2	6	6	3	17
Yellowstone National Park								
Male	4	2	(50.0)	0	0	0	1	1
Female	38	6	(15.8)	0	1	0	2	3
Both	42	8	(19.0)	0	1	0	3	4
Teton Wilderness								
Male	4	2	(50.0)	0	0	0	0	0
Female	11	2	(18.2)	0	0	0	0	0
Both	15	2	(26.7)	0	0	0	0	0
Gros Ventre drainage								
Male	2	1	(50.0)	0	0	0	0	0
Female	15	5	(33.3)	1	0	1	1	3
Both	17	6	(35.3)	1	0	1	1	3
Total								
Male	28	7	(25.0)	1	1	0	1	3
Female	147	28	(19.0)	2	6	7	6	21
Both	175	35	(20.0)	3	7	7	7	24
Combined^b								
Male	10	5	(50.0)	0	0	0	1	1
Female	64	13	(20.3)	1	1	1	3	6
Both	74	18	(24.3)	1	1	1	4	7

^aElk that were monitored for more than one hunting season were available to hunters each year. The sample sizes in the table equal the sum of all years that each elk was available to hunters.

^bYellowstone National Park, Teton Wilderness, and Gros Ventre drainage combined.

when hunting seasons were designed primarily to harvest antlerless elk in Grand Teton National Park. Antlered elk have composed 60–70% of the harvest with either-sex permits in Hunting Units 75–77 and 79 (Wyoming Game and Fish Department, 1978–86. Annual Big Game Completion Reports, unpublished). From 1981 to 1984, when male and female elk were radio-collared, antlerless permits composed 72% of the total permits issued for Hunting Units 75–77 (Fig. 3; Appendix C). The remaining 28% were issued for elk of either sex. The emphasis on antlerless elk was to expedite the reduction of the number of elk on the National Elk Refuge, particularly those from the

Grand Teton National Park herd segment. Antlerless elk were 64% of the harvested elk in those units during 1981–84 (Table 13). The composition of the harvested radio-collared elk, standardized for sample sizes, was 62% antlerless elk.

Outside Grand Teton National Park, hunting seasons were designed for the harvest of primarily male elk. From 1978 to 1983, elk hunting with general licenses was only for antlered elk, except during a portion of the season when antlerless elk also could be killed. In Hunting Units 82 and 83 in the Gros Ventre drainage, antlerless elk could be harvested only with limited quota permits (Appendix C).

Harvests in Hunting Units 75–77 were directed at the Grand Teton National Park herd segment, and the antlered-to-antlerless-elk-harvest ratio (radio-collared elk and all harvested elk) was lower there than in the Yellowstone National Park, Teton Wilderness, or Gros Ventre Drainage herd segments, which were primarily harvested in Hunting Units 70, 71, 80, 81, 82, and 83 (Table 13; Fig. 3). As a result, summer mature-male-to-female-elk ratios in the Grand Teton National Park central valley increased from a mean of 46:100 (SE = 9.2) during 1969–76 (when either-sex-elk permits were the rule) to a mean of 186:100 (SE = 23.5) during 1977–84 ($P < 0.01$; Table 4).

Post-1975 male-to-female-elk ratios on the National Elk Refuge, where the elk of the Grand Teton National Park herd segment winter, confirm the upward trend but not the magnitude in Grand Teton National Park valley male-to-female-elk ratios. In contrast, mature male-to-female-elk ratios on the Gros Ventre feed grounds (where elk from only the Gros Ventre drainage, Yellowstone National Park, and Teton Wilderness herd segments winter) averaged only 3:100 (SE = 0.4) and remained relatively stable (Table 4).

Harvests in the Jackson Herd Unit After 1983

After 1983, hunting regulations in Grand Teton National Park (Hunting Units 75, 76, and 79) and on the National Elk Refuge (Hunting Unit 77) were drastically changed (Appendix C). From as many as 8,413 elk during winter 1977–78, the number of elk on the National Elk Refuge declined to 5,010 during winter 1983–84, which was well below the targeted population size of 7,500 (Table 4). To increase the number of elk on the refuge, all hunting permits for Hunting Units 75–77 during 1984–86 were for elk of either sex (antlerless-only-elk permits were eliminated), and the number of permits was reduced (Appendix C). Hunting Unit 79 permits were reduced from an average of 2,583 during 1978–83 to 1,800 in 1984, 1,000 in 1985, and 1,500 in 1986. Antlerless animals were hunted only under limited-quota permits in Hunting Units 70, 71, 80, 81, 82, and 83 (Appendix C; Fig. 3). These conservative regulations increased the National Elk Refuge population to 7,820 elk during winter 1986–87 and to 9,486 elk (15,000 total in the Jackson herd unit) during winter 1988–89.

Whereas 73% of the harvested elk in Hunting Units 75–77 in 1984–86 were males, only 22% were males in 1978–83. As a result, classification counts in Grand Teton National Park revealed a decline in the mature-male-to-100-female-elk ratios (186 ± 23.5 in 1977–84 to 91 ± 23.3 in 1985–87; Table 4; $F = 5.28$; 1, 7 df; $P = 0.055$). During the corresponding winters, mature-male-to-100-female-elk ratios on the National Elk Refuge declined from 34.0 ± 1.5 to 22.4 ± 2.8 ($F = 16.29$; 1, 7 df; $P = 0.005$). Throughout 1978–86, male-to-female-elk ratios on the National Elk Refuge correlated ($r = 0.87$, 6 df, $P < 0.01$) with the percent of antlerless elk in the harvest from Hunting Units 75–77, which correlated ($r = 0.96$, 7 df, $P < 0.01$) with the percent of antlerless permits.

Location of Harvest by Herd Segment

During 1979–83, most elk migrated to the National Elk Refuge before the close of the hunting seasons (Table 7; Fig. 7). Of the 17 radio-collared elk harvested in Hunting Units 75, 76, and 79 (Grand Teton National Park) and 77 (National Elk Refuge) prior to 1 December, 14 were from the Grand Teton National Park herd segment (Table 12). This mirrored the earlier arrival at the National Elk Refuge of the Grand Teton National Park herd segment than the elk from other herd segments (Table 7). All harvested radio-collared elk of the Grand Teton National Park herd segment were killed in the park or on the refuge. Seven of 18 elk harvested from the other three herd segments were killed in the park or on the refuge; four of those were harvested after 30 November (Table 12).

Harvest rates were not different of elk of the Teton Wilderness and Yellowstone National Park herd segments that migrated along eastern (national forest lands) migration routes than of elk migrating along western (Grand Teton National Park) routes ($Z = 0.92$, $P = 0.18$). Whereas 7 (25%) of the 28 radio-collared elk that migrated along western migration routes were harvested, only 2 (13%) of the 15 radio-collared elk that migrated east of Grand Teton National Park were harvested.

Natural Mortality

During the 6 years we monitored radio-collared elk, 10 of the 97 animals (3 of 17 males and 7 of 80

Table 13. Harvests of elk (*Cervus elaphus*) in the Jackson herd unit^a and Grand Teton National Park and on the National Elk Refuge, Wyoming, 1950–1986.

Year	Total harvest in Jackson herd unit						Harvest in Grand Teton National Park and in the National Elk Refuge						
	Total	Antlered		Antlerless		Unknown	Hunting units			Hunting units 75-77			
		no.	%	no.	%		77 ^b no.	75,76,79 ^c no.	Total	Antlered no.	Antlerless no.	%	
1950	3,638	1,256	42	1,762	58	620							
1951	4,810	1,469	36	2,567	64	774		184					
1952	2,108	771	42	1,080	58	257	210	27					
1953	2,823	957	45	1,166	55	700	67	112					
1954	2,594	1,113	46	1,301	54	180		104					
1955	3,207	1,234	40	1,848	60	125		310					
1956	3,106	1,028	33	2,078	67	0		325					
1957	2,252	713	38	1,164	62	375		160					
1958	3,057	1,250	41	1,807	59	0		110					
1959	1,542	703	46	832	54	7		0					
1960	2,074	767	44	977	56	330		0					
1961	2,639					2,639		278					
1962	1,320	684	55	554	45	82		280					
1963	2,996	1,608	56	1,284	44	104	95	625	496				
1964	2,975	1,534	53	1,373	47	68	50	753	611				
1965	3,250	1,775	56	1,397	44	78	96	691	570				
1966	3,226	1,907	59	1,319	41	0	133	612	306				
1967	2,974	1,879	63	1,095	37	0	131	375	286				
1968	3,090	1,776	43	2,383	57	26	68	520	351				
1969	3,444	1,873	54	1,571	46	0	148	568	529				
1970	5,680	2,618	46	3,055	54	7	162	828	592				
1971	4,245	1,608	38	2,583	62	54	70	584	366	98	268	73	
1972	4,086	1,666	41	2,420	59	0	59	519	553	235	318	58	
1973	4,684	1,908	41	2,776	59	0	77	571	306	76	230	75	
1974	2,774	1,033	38	1,681	62	0	49	451	185	77	108	58	
1975	3,526	1,631	46	1,895	54	0	139	701	651	338	313	48	
1976	1,429	670	47	759	53	0	0	293	113	0	113	100	
1977	3,756	1,799	48	1,957	52	0	220	642	505	0	505	100	
1978	2,880	1,131	39	1,749	61	0	227	659	512	0	512	100	
1979	3,321	1,225	37	2,096	63	0	280	691	801	34	767	96	
1980	3,740	1,847	49	1,893	51	0	513	492	629	312	317	50	
1981	4,290	1,964	46	2,326	54	0	481	501	614	163	451	73	
1982	3,548	1,343	38	2,205	62	0	323	870	636	110	526	83	
1983	2,355	1,165	49	1,190	51	0	317	618	488	124	364	75	
1984	1,524	1,087	71	437	29	0	132	372	250	189	61	24	
1985	1,368	1,009	56	796	44	0	178	343	335	237	98	29	
1986	1,254	977	76	317	24	0	140	344	203	149	54	27	
Mean	3,016	1,361	46	1,602	54	173	174	456	454	165	313	67	

^a 5,195 km² in the Snake River watershed.^b There was not a hunt in Hunting Unit 77 in 1950, 1951, and 1954–62.^c Includes harvests from Hunting Unit 72 in Grand Teton National Park 1951–62. Before 1963 Hunting Units 75 and 76 in Grand Teton National Park were not open to hunting. Unit 75 was closed to hunting 1974–76.

females) died of causes believed to be unrelated to hunting. Six of 10 (2 males and 4 females) died on the National Elk Refuge between November and May. The other four died on summer ranges between July and November. The summer ranges of

8 of the 10 dead elk were known. Four summered in Grand Teton National Park and 4 summered in the Teton Wilderness.

Causes of death could not be determined from the skeletal remains. One female elk that summered in

the Teton Wilderness and died on the refuge in April 1983 had been immobilized during the previous month to replace her radio collar. At that time she was emaciated and suffered from a swollen right-front knee joint and laminitis of a swollen left-rear foot on which the hoof was 40 cm overgrown. Judging by tooth wear, she was >15 years old. A male that summered in Grand Teton National Park had severe alopecia because of scabies mites (*Psorptes equi cervinus*) and was emaciated when he died on the refuge in March 1983. His age from tooth cementum analysis was 7.5 years at that time. He did not have clinical scabies when radio-collared in March 1981. Another male elk that summered in the Teton Wilderness had clinical scabies when he died on the National Elk Refuge in November 1981 but not when he was radio-collared in the previous spring. According to tooth wear, he was 3.5 years old in spring 1981.

Survival

Survival of the radio-collared elk from Grand Teton National Park was higher than survival of elk from the other three herd segments combined ($X^2 = 17.651$, 9 df, $P = 0.04$; Table 14). The difference in

survival between radio-collared elk that summered in national parks and those that summered in the national forest approached statistical significance ($X^2 = 26.40$, 17 df, $P = 0.07$). Survival did not differ between males ($\bar{x} = 0.630$, $n = 18$, $X^2 = 2.503$, 1 df, $P = 0.11$) and females ($\bar{x} = 0.778$, $n = 69$; Table 14).

Discussion

Distribution

Summer Distribution of Elk

Cole (1969) estimated that in 1964 approximately 70% of the elk that wintered on the National Elk Refuge summered in Yellowstone National Park and Grand Teton National Park. Fifteen to 20 years later, approximately 76% summered in Yellowstone National Park and Grand Teton National Park (based on the distribution of radio-collared elk). Although the Yellowstone National Park herd segment seemingly declined ($Z = 18.28$, $P < 0.001$) from 42% to approximately 28% of the elk wintering on the refuge, the Grand Teton National Park herd

Table 14. Survival rates of elk (*Cervus elaphus*) of the Jackson elk herd, estimated with Program SURVIV (White 1983). Data are presented by herd segment, each of which is identified by its summer range.

Herd segment (summer range)	N	Sex	S ^a	SE	95% CI
All ^b	85	M & F	0.754	0.034	0.688–0.820
All ^b	68	F	0.778	0.035	0.709–0.847
All ^b	17	M	0.630	0.095	0.443–0.816
Grand Teton National Park	32	F	0.803	0.091	0.625–0.981
Yellowstone National Park	21	F	0.819	0.087	0.649–0.989
Teton Wilderness	6	F	0.709	0.158	0.399–1.000
Gros Ventre drainage	9	F	0.654	0.267	0.131–1.000
Grand Teton and Yellowstone national parks	53	F	0.811	0.060	0.693–0.929
Teton Wilderness and Gros Ventre drainage	15	F	0.681	0.103	0.479–0.883

^a Survival rates.

^b All segments.

segment has increased ($Z = 24.36$, $P < 0.001$) from 29% (Cole 1969) to approximately 48% (this study).

Fidelity to the Jackson Herd Unit

Elk of the Yellowstone National Park herd segment share portions of their summer range with elk from the northern herd of Yellowstone National Park, the Shoshone River herd of Wyoming, and the Sand Creek herd of Idaho (Anderson 1958; Craighead et al. 1972; Rudd et al. 1983; C. Brown 1985 Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished). Only one radio-collared elk left the Jackson herd unit during 1978–84. In 1981–82, that female elk wintered 16 km south of the National Elk Refuge at the Horse Creek feed ground. She returned to the National Elk Refuge in the following two winters. Based on migrations of radio-collared elk (B. Long, M. Hinschberger, G. Roby, and J. Kimball. 1980. Gros Ventre cooperative elk study: final report 1974–1979. Wyoming Game and Fish Commission, unpublished; this study) and returns of ear tags (Straley 1968; Boyce 1989), the boundaries of the Jackson herd unit, except perhaps for southwestern Yellowstone National Park, remain unchanged from earlier delineations (Anderson 1958; Cole 1969).

Fidelity to Seasonal Ranges

Strong fidelity to seasonal ranges, demonstrated by the radio-collared elk, also has been reported by other authors (Anderson 1958; Craighead et al. 1972; Houston 1982; Hershey and Leege 1982; Rudd et al. 1983; C. Brown 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished). The fidelity of the elk to migration routes and summer ranges has major implications for the management of the Jackson elk herd. The traditional use of seasonal ranges by individual elk and by distinct herd segments, which is also reported of the migratory Sand Creek herd (C. Brown, 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished) and of various elk herds in Montana (L. J. Lyon, T. N. Lonner, J. P. Weigand, C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleery, and L. L. Hicks. 1985. Coordinating elk and timber management: final report of the Montana Cooperative

Elk-Logging Study, 1970–1985. Montana Department Fish Wildlife and Parks, unpublished), may be a consequence of matrilineal fidelity to ranges by young (Murie 1951; Clutton-Brock et al. 1982). This underscores the need to manage herd segments on distinct summer ranges.

Present objectives for the Jackson herd specify a posthunting-season population of 11,000 elk distributed as follows: 2,400 at the three Gros Ventre drainage feed grounds, 7,500 at the National Elk Refuge, and about 1,100 elk on winter ranges other than those feed grounds. Elk from two or more herd segments attend each feed ground and the other winter ranges (Figs. 2, 6). The size of each herd segment on the summer ranges cannot be inferred from the number of elk at feed grounds. Theoretically all 7,500 elk that winter on the National Elk Refuge could summer, for example, in Grand Teton National Park, and management objectives would be met. If the state and federal agencies seek to restore pre-1950 distributions of elk on summer ranges, then it is necessary to establish numeric objectives for herd segments on each summer range. Hunting seasons in each hunting unit should then be designed to achieve the desired size and composition of each herd segment.

Migration

Migrations Through Grand Teton National Park

The distributions of migrating elk have been estimated since 1945 by counting tracks that cross Highway 26/287 between Moose, Wyoming, and the Togwotee Pass (Fig. 1). Although numbers of elk and proportions of each herd segment that follow various migration routes may have changed during the past 4 decades, the geographical location of the routes have remained much the same as Anderson (1958) described them.

Cole (1969) reported that 32% of the elk tracks to winter ranges in 1949, 42% in 1957, and 75% in 1964 crossed through Grand Teton National Park. Tracks of neither the Gros Ventre herd segment nor of most elk of the Grand Teton National Park herd segment that migrate to the National Elk Refuge are counted because of the location of the transects. The track counts reflect east to west distributions of elk of the Teton Wilderness and

Yellowstone National Park herd segments that migrate through the Jackson herd unit. Recent analyses of the track-count data revealed that 40% of the elk in the Jackson herd unit in the 1950s, 60% in the 1960s, 71% in the 1970s, and 72% in the 1980s migrated through Grand Teton National Park to reach their winter ranges (Boyce 1989). The remainder migrated through national-forest lands east of Grand Teton National Park (Fig. 6).

The migrations of radio-collared elk in our study corroborate the findings of increased migration of elk through Grand Teton National Park during the 1970s and 1980s. Seventy-one percent of the radio-collared elk that summered in Yellowstone National Park or in the Teton Wilderness during this study passed through Grand Teton National Park. Bendt (1962), Cole (1969), Johnson (1976), and Toman (1987) attributed the decline of elk that summer in the eastern Teton Wilderness and in eastern Yellowstone National Park to differential harvests along the eastern migration routes that increased from improved vehicle access for logging in the Bridger-Teton National Forest.

Behavioral Responses to Hunting

Elk of the Grand Teton National Park and Yellowstone National Park herd segments that summered adjacent to national-forest lands did not cross park boundaries until migration began. Furthermore, the only two elk that summered in the Teton Wilderness near the southern border of Yellowstone National Park moved into refuge areas in late summer. One female elk moved 0.5–9.0 km north into Yellowstone National Park between 9 and 22 September during each of 5 years. The other moved 1–8 km into Yellowstone National Park between 10 and 22 September during each of 3 years. Hunting seasons in the Teton Wilderness opened on 10 September each year, and Teton Wilderness outfitters have noted similar behavior in elk during mid-September (R. Johnson, outfitter, Kelly, Wyoming, personal communication, 1989). Instances of elk moving from areas open to hunting to adjacent refuge areas at the onset of hunting seasons have been reported in Montana (Knight 1970), Idaho (C. Brown, 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game,

unpublished), and British Columbia (Morgantini and Hudson 1988).

Reduced Migration of Elk from Southwestern Yellowstone National Park

Cole and Yorgason (G. F. Cole and I. J. Yorgason. 1965. Elk migration study, Jackson Hole elk herd, 1965. U.S. National Park Service and Wyoming Game and Fish Commission, unpublished) reported that at least 578 elk migrated from southwestern Yellowstone National Park along the shores of Jackson Lake to the National Elk Refuge in 1964. Cole (1969) believed that 800 of the elk that wintered on the National Elk Refuge migrated to summer ranges in southwestern Yellowstone National Park. Aerial surveys indicated that migration had dwindled to 100–150 elk by the late 1970s and was no larger during the 1980s (G. Roby, Wyoming Game and Fish Department, and R. Wood, Grand Teton National Park, personal communication). No locations of radio-collared elk were obtained west of Highway 89/287 in Yellowstone National Park during this study.

Excessive elk harvests have not been reported along migration routes between southwestern Yellowstone National Park and Grand Teton National Park. However, the apparent decline of migrating elk from southwestern Yellowstone National Park during the 1970s coincided with an increase in the number of wintering elk in the adjacent Sand Creek area of eastern Idaho (C. Brown, 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished). Empirical evidence of a shift in migration routes and winter ranges of elk from southwestern Yellowstone National Park is lacking.

Implications for Harvests

As reported of other elk herds (Craighead et al. 1972; Adams 1982; Hershey and Legee 1982; Rudd et al. 1983; C. Brown, 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished), fall migrations were stimulated by snow accumulations at high elevations on summer ranges. Elk from the more distant summer ranges in Yellowstone National Park, the Teton Wilderness, and northwest Grand Teton National Park arrived significantly later (6–15 days) at the National Elk Refuge than elk from the Grand Teton National Park valley

because of the longer duration of the migration. This provided an opportunity to harvest primarily elk of the Grand Teton National Park valley herd segment in Hunting Units 75, 76, and 77 during the early stages of migration.

Calving

Fidelity to Calving Areas

The fidelity of radio-collared elk to calving areas was related to each calving area's elevation and distance from the winter range and to annual weather patterns. In years with early snowmelt, as in 1981, more elk may calve in Yellowstone National Park, northern areas of Grand Teton National Park, and the Teton Wilderness. The interaction of elevation and temperature probably influenced winter snowpack, spring soil temperatures, and consequent greening of vegetation. Greening is not prevented by a lack of soil moisture because moisture from snowmelt and precipitation are abundant during May, the second wettest month of the year.

As reported by Brazada (1953), residual snowpack in spring alone did not deter migration of some elk to calving areas. We observed elk crossing snow-covered areas during migration to reach areas with new vegetative growth.

Results of our investigation of the Yellowstone National Park, Teton Wilderness, and Gros Ventre Drainage herd segments support Murie's (1951) conclusion that most young are born somewhere between the winter and summer ranges. In response to the growth in the Grand Teton National Park herd segment since 1950 and the short migration time between their winter and summer ranges, however, many elk now calve on their summer ranges. Calving on the National Elk Refuge, as reported by Murie (1951) and Altmann (1952), was not observed during this study and has probably been rare since the 1960s (unpublished National Elk Refuge annual narrative reports). Most elk that remained on the National Elk Refuge during summer were 1-year-old individuals.

Grand Teton National Park Valley Calving Area

Although we identified seven calving areas during this study, 69% of the radio-collared female elk used only the Grand Teton National Park valley

calving area during 1978–83. Another 13% used the Grand Teton National Park valley and an adjacent calving area. This apparent attraction to the Grand Teton National Park valley calving area has several possible explanations:

1. The expansive, snow-free mosaic of aspens, sagebrush, conifers, and meadows in Grand Teton National Park provides suitable habitat for calving (Skovlin 1982). Similar habitat was less abundant in the other calving areas. The valley was mostly free of snow by mid-May and provided ample green forage for pregnant and lactating females. Metabolizable energy requirements of pregnant females increase markedly during late pregnancy. Requirements continue to rise until about 48 days postpartum when energy expenditure for lactation exceeds maintenance requirements by nearly 60% (Moen 1973; Nelson and Legee 1982).
2. The six calving centers in the Grand Teton National Park valley calving area were in the summer ranges of the Grand Teton National Park valley herd segment (Fig. 8).
3. Spring migrations of most elk that summered in northwest Grand Teton National Park, Yellowstone National Park, and the Teton Wilderness passed through the Grand Teton National Park valley. If snows were still deep farther north, which is normal in Jackson Hole, a larger proportion of those elk calved in Grand Teton National Park valley than farther north. Variation in calving locations because of late snowmelt and greening of vegetation was previously reported of elk in Jackson Hole (Altmann 1952; Anderson 1958; and Cole 1969), Montana (Knight 1970; Sweeney and Steinhoff 1976), Idaho (C. Brown, 1985. Sand Creek elk: population status, movement, and distribution. Idaho Department of Fish and Game, unpublished), and Yellowstone National Park (Houston 1982).
4. In 1958, grazing of livestock ceased in calving areas west of the Snake River in Grand Teton National Park. Several authors reported that elk avoid cattle and that cattle displace elk (Skovlin et al 1968; T. N. Lonner, 1975. Elk-cattle distribution and interspecific relationships. Long Tom Creek Study, Montana, Montana Cooperative Elk/Logging Study Annual Progress Report, unpublished; Sauer 1980; L. J. Lyon, T. N. Lonner, J. P. Weigand,

C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleery, and L. L. Hicks. 1985. Coordinating elk and timber management: final report of the Montana Cooperative Elk-Logging Study, 1970–1985. Montana Department Fish Wildlife and Parks, unpublished).

5. With the exception of early-season tourists along roadways and points of interest, Grand Teton National Park provides elk with security from human disturbance.

Calving Areas Beyond the Grand Teton National Park Valley

The Grand Teton National Park valley calving area was used by female elk from every summer herd segment, but the other six calving areas were used exclusively by elk that summered outside the Grand Teton National Park valley. Consequently, preserving the integrity and security of those calving areas (B. Long, M. Hinschberger, G. Roby, and J. Kimball. 1980. Gros Ventre cooperative elk study: final report 1974–1979. Wyoming Game and Fish Commission, unpublished; Kuck et al. 1985) is paramount to the maintenance of the Yellowstone National Park, the Teton Wilderness, and the Gros Ventre herd segments. The Mount Randolph, Slate Creek, and eastern Spread Creek-Uhl Hill calving areas are of special concern because most of those lands do not have the formal protection of national-park and national-wilderness-area designations.

The North Jackson Lake or Yellowstone National Park Snake River calving areas were not reported in previous accounts of the Jackson elk herd (Altmann 1952; Anderson 1958; Murie and Murie 1966). Elk from winter ranges other than the National Elk Refuge calve in additional areas of the Bridger-Teton National Forest and southern Yellowstone National Park. North (D. North, 1991. The Buffalo Valley Elk Enhancement Project. 1990 Annual Report, Wyoming Game and Fish Department, unpublished) captured and radio-collared 11 female elk on their winter ranges 30–35 km north of the National Elk Refuge in the Buffalo River valley. During 1990, 9 of the 11 female elk calved—2 in southeastern Yellowstone National Park, 1 south of the Teton Wilderness, 4 in the eastern the Teton Wilderness, and 2 others probably also in the Teton Wilderness.

Sympatry and Diseases of Wildlife and Livestock

Elk, bison, and domestic cattle are susceptible to brucellosis—the only known, reportable (Code of Federal Regulations, Title 9, Part 161.3(f)) disease of the Jackson elk herd that is potentially transmissible to livestock and humans (Thorne et al. 1991; Smith and Roffe 1994). The most important clinical sign of this bacterial infection in elk, bison, and cattle is spontaneous abortion (Thorne et al. 1982; Davis et al. 1988). Elk and bison of the Yellowstone ecosystem harbor *Brucella abortus* biotypes 1, 2, and 4—the same bacterium and biotypes that are responsible for most bovine brucellosis (Thorne et al. 1991). A national program to eradicate brucellosis was initiated in 1935 by the U.S. Department of Agriculture. The department places commerce restrictions on livestock operators whose animals contract the disease. Infected livestock herds must be quarantined and retested after 60 days, and subsequent reactors must be slaughtered. Shipment of animals from the herd, except for slaughter, is prohibited.

Strain 19, a live vaccine of *B. abortus*, has been in use for over 40 years. It is considered 60–70% effective in preventing abortion and 55–65% effective in averting field-strain infections in cattle that were vaccinated as young (Manthei 1952, 1959). Tests and slaughter of reactors and vaccination have been the only successful means of eliminating brucellosis in infected herds (Manthei 1959; Davis et al. 1991).

Brucellosis in Elk

Brucellosis was first diagnosed in 3 of 9 serologically tested elk in Jackson Hole in 1930 (Murie 1951). Since then, free-ranging elk have represented a potential source of brucellosis for sympatric domestic livestock in late pregnancy or at parturition. The average infection rates since 1970 have been 39% of females and 28% of all wintering elk on the National Elk Refuge (E. T. Thorne, unpublished in Boyce 1989). Blood tests and tissue cultures also revealed brucellosis in elk or their aborted fetuses at 18 state-operated feed grounds in western Wyoming (Thorne et al. 1991). Only elk in the northern range of Yellowstone National Park (1.7% of 6,027 tested elk during



Intentional or incidental feeding of elk with cattle on private lands during late winter and during spring increases the risk of interspecific transmission of brucellosis in western Wyoming; February 1992.

1960–68, M. Meagher, Yellowstone National Park, personal communication, 1989), which are sympatric with infected bison, maintain the disease in the absence of winter feeding programs (Smith and Roffe 1994).

A 50% probability exists that a female elk aborts her first pregnancy after infection with brucellosis. Thereafter, she will probably reproduce successfully but will remain a carrier of the disease and continue to shed *B. abortus* in vaginal exudates, live births, and afterbirths (Thorne et al. 1982). This represents a 7% (Oldemeyer et al. 1993) to 12% (Thorne et al. 1979) reduction in the annual fecundity.

Brucellosis in Bison

The Jackson bison herd, which numbered 107 animals in winter 1987–88, has wintered on the National Elk Refuge since 1975 and feeds on natural forage and supplemental feed with the elk (Grand Teton National Park, National Elk Refuge,

Wyoming Game and Fish Department, and Bridger-Teton National Forest. 1994. The Jackson bison herd: long-term management plan and environmental assessment. Grand Teton National Park, unpublished). In 1988 and 1989, 76% of 35 bison that were culled from the herd were serologically positive or suspected of having *Brucella* antibodies. Of the serologic reactors that were cultured for *B. abortus*, 36% were positive (Williams et al. 1993). The seroprevalence in bison from the northern range of Yellowstone National Park is 54% (H. I. Pac and K. Frey. 1991. Some population characteristics of the northern Yellowstone bison herd during the winter of 1988–1989. Montana Department of Fish, Wildlife and Parks, unpublished). There is ample opportunity for interspecific exposure of bison and elk to *B. abortus* because aborted fetuses of both species have been observed on the National Elk Refuge (Thorne et al. 1982; Oldemeyer et al. 1993; Williams et al. 1993).

Transmission of Brucellosis

Transmission of brucellosis from infected elk and bison to susceptible domestic cows has been demonstrated (Thorne et al. 1979; Davis et al. 1988). Transmission is possible where infected and susceptible animals are closely associated. Transmission of brucellosis from infected elk or bison to cattle has not been documented in western Wyoming and the Yellowstone ecosystem (Thorne et al. 1982; Thorne et al. 1991). Areas in the Jackson herd unit where transmission of brucellosis from wildlife to livestock could occur are winter and spring ranges of elk and bison. Neither species is in contact with cattle on either the National Elk Refuge or Gros Ventre Drainage feed grounds or on other winter ranges in Grand Teton National Park or the Bridger-Teton National Forest. Elk occasionally feed with livestock on private lands in winter, primarily in the Buffalo Valley east of Moran, Wyoming. This practice should be steadfastly discouraged.

As elk and bison migrate from the National Elk Refuge in spring, they travel through private inholdings and cattle-grazing allotments in Grand Teton National Park (Figs. 6, 9, 10). During the second week of June, 2,500 head of cattle are trailed east to the Gros Ventre Mountains on a stock drive trail in Grand Teton National Park adjacent to the National Elk Refuge. Most elk migrate in advance of this date, but bison often linger in the vicinity of the drive trail near Kelly, Wyoming. Another 800 cattle are trailed to the Blackrock-Spread Creek allotment and 235 to the Ditch Creek allotment during early June. Cattle may encounter elk or bison in those allotments, but the stock driveways are not significant calving areas (Fig. 10).

Cattle again trail through those stock driveways during the last half of October. Bison often graze the driveways in October, but the potential for transmission of brucellosis from bison or elk to cattle is remote during fall.

Elk and bison calve primarily in May and June (Johnson 1951; Murie 1951; Meagher 1973; Oldemeyer et al. 1993), although late-born offspring of both species have been observed during fall on the National Elk Refuge (Grand Teton National Park, National Elk Refuge, Wyoming Game and Fish Department, and Bridger-Teton National Forest.

1994. The Jackson bison herd: long-term management plan and environmental assessment. Grand Teton National Park, unpublished; Smith 1994). Distributions of elk, cattle, and bison overlap on many cattle-grazing allotments in Grand Teton National Park and in the Bridger-Teton National Forest. Cattle also share ranges with calving elk (that winter on the three Gros Ventre Drainage feed grounds) on several additional allotments in the upper Gros Ventre drainage (B. Long, M. Hinschberger, G. Roby, and J. Kimball. 1980. Gros Ventre cooperative elk study: final report 1974–1979. Wyoming Game and Fish Commission, unpublished; unpublished Bridger-Teton National Forest files; Fig. 10). Cattle herds on most private lands in Grand Teton National Park or adjacent to elk calving areas in the Bridger-Teton National Forest likewise risk contact with *B. abortus*. In allotments where grazing by livestock coincides with the 25 May–15 June peak of elk parturition, the risk of brucellosis transmission to livestock is greatest on federal lands (Appendix D). Where grazing of allotments begins later, cattle avoid the peak parturition period of both elk and bison.

Significance of Brucellosis in Jackson Hole

The economic and political significance of brucellosis in the Jackson elk herd in a state where all livestock is certified by the U.S. Department of Agriculture as free of brucellosis clearly outweighs the biological importance of the disease in elk. The Jackson elk herd continues to thrive and provides an annual harvest of 2,500–3,000 animals and unparalleled opportunities for nonconsumptive recreation (Smith 1991). It also provides a persistent reservoir of *B. abortus*.

Despite considerable opportunity for contact between cattle, elk, and bison, records (D. Woody, U.S. Department of Agriculture, Veterinary Services, personal communication, 1987) that begin in 1951 show that only a single case of brucellosis in cattle that may be traceable to wild ungulates has occurred in Teton County, Wyoming. That case was discovered during fall 1984 in a small herd of Hereford cattle 11 km north of Jackson. Doubt remains whether this was an actual field-strain brucellosis infection or a vaccination phenomenon (e.g., inadvertent revaccination or infection with vaccine strain *B. abortus*). Attempts to culture organisms from tissues of reactors were unsuccessful

(D. Woody, U.S. Department of Agriculture, Veterinary Services, personal communication, 1987).

A 1988 infection of a cattle herd east of the Jackson herd unit in Fremont County, Wyoming, generated a litigation for economic loss against several federal and state agencies (Keiter and Froelicher 1993). Elk and bison from Jackson Hole were the alleged source of the infection. The U.S. District Court of Wyoming ruled in favor of the U.S. Government in April 1992. The Wyoming Supreme Court ruled in favor of the state in January 1993. In both cases, convincing evidence was not presented that either elk or bison were the source of the disease in cattle.

Wyoming, Montana, and Idaho are certified as free of brucellosis by the U.S. Department of Agriculture and as such are free of mandatory testing and vaccination of livestock. The livestock industry and the states are sensitive to any threats to that status. Although the probability of transmission to a domestic cow from a wild ungulate seems very low (Thorne et al. 1991; Smith and Roffe 1994), the consequences are substantial for not only the livestock operator but for all producers who risk restrictions of the transfer and sales of their herds. As U.S. Department of Agriculture Veterinarian Douglas Woody (personal communication, 1987) noted:

As the goal of cattle brucellosis eradication is approached, increased attention is being focused on wildlife brucellosis by livestock health officials. The risk of wildlife-to-cattle brucellosis transmission has probably not increased, but the stakes are higher than before.

Survival

The mean annual survival rate of female elk in the Jackson herd unit (0.778) was not significantly different from the rate reported by Straley (1968) who used the composite dynamic method ($\bar{x} = 0.742$) and by Sauer and Boyce (1983) who used program BROWNIE ($\bar{x} = 0.590$ during 1958–59; $\bar{x} = 0.679$ during 1962–66). Those authors calculated survival rates from returned ear tags. Elk harvests were lower in the 1950s and 1960s than during the present study (Tables 14, 15).

The survival rate of male elk in 1978–84 that we calculated (0.63) was similar to the survival rate (0.65) that Straley (1968) calculated of male elk in the 1960s. Estimated survival rates during the early 1950s ($\bar{x} = 0.378$) and late 1950s ($\bar{x} = 0.536$) were not significantly different because of their large standard errors (Sauer and Boyce 1983). Sauer and Boyce (1983) noted that their mean estimates of survival may have been biased because they eliminated data from years when few elk were tagged. Furthermore, our sample was from a period when the harvest of antlerless elk was emphasized (Appendix C).

Harvests of Elk and Population Regulation

Management of the Jackson elk herd requires the cooperative efforts of several federal and state agencies. In 1958, the Jackson Hole Cooperative Elk Studies Group, an interagency working group composed of the Wyoming Game and Fish Department, National Park Service, U.S. Forest Service, and U.S. Fish and Wildlife Service, was formed to address research and management issues (Robbins et al. 1982). A primary goal of cooperative management was to restore historic (pre-1950) summer distributions and migrations of elk in the Jackson herd unit (Cole 1969; National Park Service. 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment, unpublished).

Reasons for Hunting on the National Elk Refuge

Hunting began on the refuge in 1943 to reduce the number of wintering elk on the refuge (11,000 in winter 1942–43) and a growing summer herd (>500 in summer 1943; J. G. Griffin, 1985. Elk Hunting Plan National Elk Refuge. National Elk Refuge, unpublished). The refuge manager sought to avoid mass starvation of the wintering elk by reducing herd size because hay purchased annually for feeding the elk was needed for cattle to help with the national shortage of meat during World War II. Since the late 1960s, an increasingly important function of the refuge hunt has been to assist the state of Wyoming with reducing the number of elk that migrate to the refuge from

Table 15. Number of harvested elk (*Cervus elaphus*) in the Jackson herd unit^a during 1950–1986 and the estimated number of elk in the central valley of Grand Teton National Park in subsequent summers. The estimated mean numbers of elk during 1964–1968 are significantly less ($P < 0.001$) than the mean numbers of elk during all later periods. The remaining mean numbers of elk do not differ from each other.

Years	Management emphasis	Total harvest Mean $\pm$ sd	Number of harvested elk in Grand Teton National Park and on the National Elk Refuge		Estimated number of elk in the central valley of Grand Teton National Park	
			Mean $\pm$ sd	% of total	Years	Mean $\pm$ sd
1950–62	Moderate culling of elk in Grand Teton National Park	2,705 $\pm$ 917	167 $\pm$ 116	6.2	1951–63	N/A ^b
1963–67	Stabilization of number of elk in Grand Teton National Park	3,084 $\pm$ 141	812 $\pm$ 120	23.1	1964–68	1,114 $\pm$ 25 ^c
1968–77	Heavy harvests to control total number of elk in the Jackson herd unit	3,671 $\pm$ 1,146	667 $\pm$ 199	18.2	1969–78	1,562 $\pm$ 293 ^c
1978–83	Reduction of the numbers of elk in Grand Teton National Park	3,356 $\pm$ 676	994 $\pm$ 106	29.6	1979–84	1,560 $\pm$ 155 ^c
1984–86	Years of reduced harvest in the Jackson herd unit to increase numbers of elk on the National Elk Refuge but stabilize numbers in Grand Teton National Park	1,382 $\pm$ 136	507 $\pm$ 28	36.7	1985–87	1,583 $\pm$ 313 ^{d,e}

^a 5,195 km² in the Snake River watershed.

^b No herd size estimates (Cole 1969).

^c Boyce 1989.

^d Boyce 1989 and R. Wood, Grand Teton National Park (unpublished data).

^e Excluding 1986 when fog that caused poor visibility of elk resulted in a low estimate of 836 elk (R. Wood, Grand Teton National Park, personal communication).

Grand Teton National Park (J. G. Griffin, 1985. Elk Hunting Plan National Elk Refuge. National Elk Refuge, unpublished). Hunting on the refuge is permitted under refuge regulations and is designed and conducted under a cooperative agreement between the National Elk Refuge and the Wyoming Game and Fish Department.

Reasons for Hunting in Grand Teton National Park

The legislation that expanded Grand Teton National Park in 1950, Public Law 81–787, provided hunting of elk in portions of the lands added to Grand Teton National Park "...when it is found necessary for the purpose of proper management and protection of the elk." In fact, elk have been hunted in Grand Teton National Park every year

since 1950 except in 1959 and 1960. Joint state-federal jurisdiction of elk in Grand Teton National Park and provisions in Public Law 81–787 are the basis for the cooperative management of hunting in the park. Cole (1969) listed the reasons and objectives for harvesting elk in Grand Teton National Park as follows:

1. Objective: Hunt elk in the park to reduce the number of early migrants to the refuge from the Grand Teton National Park herd segment.
Reason: Many elk that summered in Grand Teton National Park migrated to the National Elk Refuge in October and used forage reserved for consumption in winter.
2. Objective: Harvest late-migrating elk of the Yellowstone National Park herd segment to levels that eventually could be controlled by hunting

outside Grand Teton National Park.

Reason: Late-migrating elk from southern Yellowstone National Park that traveled through roadless wilderness areas before crossing Grand Teton National Park had become too numerous to manage without assistance from Grand Teton National Park.

3. Objective: Restrict harvests of elk that migrate east of Grand Teton National Park or summer on national forest lands between the two parks to foster increases in those herd segments.

Reason: Herd segments that migrated through roaded areas east of Grand Teton National Park or summered on the more accessible national forest lands between Yellowstone National Park and Grand Teton National Park had been reduced to levels that no longer represented the major portion of the elk herd.

Cole (1969) stated that objectives 1 and 2 were achieved during 1963–68. Robbins et al. (1982) confirmed that objective 1 was achieved. Our results suggest that objective 2 was also achieved. Cole (1969:50) further stated that progress was made toward achieving objective 3. He predicted "it may be possible within a few years" to relegate the role of Grand Teton National Park in the restoration of pre-1950 distributions and migrations in the Jackson herd unit to a "standby status with limited hunts when state programs need assistance." The following evaluation indicates that Cole's (1969) third objective has not been achieved.

Consequences of Harvests of Elk During 1950–1985

The Grand Teton National Park herd segment ostensibly increased during 1950–63 and 1968–78. Harvests from the combined Grand Teton National Park and National Elk Refuge hunting units during 1950–62 were only 6% of the elk harvest in the Jackson herd unit. As a result, the elk that summered in the Grand Teton National Park valley increased from a few elk prior to 1950 (Anderson 1958) and in the early 1950s (Jepson 1952) to an estimated 1,430 in 1963 (Cole 1969).

Increased harvests during 1963–67 in Grand Teton National Park and on the National Elk Refuge apparently stabilized the number of elk (Table 15). Boyce (1989) reported that after 1963, when hunting began in Hunting Units 75 and 76 in Grand Teton National Park, harvests of elk in Grand Teton

National Park inversely correlated with counts of elk in the central valley in the following summers ($r = -0.435$, $n = 22$, $P < 0.05$). Boyce (1989) did not identify a statistically significant upward trend in the number of elk in the central valley during 1963–85. However, we found that larger numbers of elk were counted in the central valley during 1969–78 than during 1964–68 ($t = 5.0$, 13 df, $P < 0.001$; Table 15). This second period of growth included 4 years of record harvests ($\bar{x} = 4,674$) in the Jackson elk herd during 1970–73, but the combined kills in Grand Teton National Park and in the National Elk Refuge were only 18% of all kills (Table 15). Based on track counts, those harvests coincided with a marked decline in the proportion of elk that occupied the eastern portions of the Jackson herd unit (W. J. Barmore, 1984. A synthesis of information on elk that summer in or migrate through Grand Teton National park. Grand Teton National Park, unpublished; Boyce 1989). The long-term goal of restoring pre-1950 distributions of elk was abandoned to hasten reductions in the number of elk on feed grounds. The number of wintering elk on the National Elk Refuge declined from 9,205 in 1969 and stabilized between 7,194 and 8,054 ($\bar{x} = 7,638$) in 1971–75 (Table 4).

Fall 1976 was extremely mild and resulted in a late migration and the lowest harvest of elk (1,429 elk) since 1962. The number of elk at the refuge grew to 8,413 during winter 1977–78. Harvest objectives from 1978 to 1983 were designed to control the size of the Jackson elk herd and to reduce the proportion of the Grand Teton National Park herd segment in the herd (Smith 1985). However, hunting seasons that extended into December generated harvest rates of the Gros Ventre Drainage, the Teton Wilderness, and Yellowstone National Park herd segments that were greater than or equal to harvests of the Grand Teton National Park herd segment. Numbers of elk on the refuge declined to 5,010 during winter 1983–84.

Mean annual harvests from the combined Grand Teton National Park and National Elk Refuge hunting units were highest during 1978–83 (Tables 13, 15). Despite increased harvests and an increased proportion of females harvested in the park and refuge, the counts of elk in the central valley have remained stable since 1977.

Evaluation of Hunts in Grand Teton National Park and on the National Elk Refuge

The Grand Teton National Park herd segment is the most difficult to harvest. About 85% of the elk in that herd segment reside in areas presently closed to hunting. Hunting Unit 72 represents 33% (19,838 of 59,514 ha) of the area where hunting is authorized by Public Law 81-787, but was opened to hunting in only 1950 and 1962-67. During those 7 years, harvests in Unit 72, which is roadless, averaged only 14 elk/year (Cole 1969), which is insignificant in the overall management of the Jackson elk herd.

The remaining hunting units in Grand Teton National Park (75, 76, and 79) and Hunting Unit 77 on the National Elk Refuge are the only locations in which elk of the Grand Teton National Park herd segment can be harvested (Fig. 3). However, the distance between the Baseline Flats staging area and the southern portion of the National Elk Refuge that is closed to hunting can be traversed in a few hours or overnight (as some elk do). Mass migrations of the Grand Teton National Park herd segment, such as the 2,700 in 1988 and 1,900 in 1989 that arrived in the closed area of the refuge within 24 h, also thwart harvest of those elk.

Recognizing that some elk of the Teton Wilderness and Yellowstone National Park herd segments in addition to elk summering in Grand Teton National Park migrate through the park and refuge hunting units, officials of Grand Teton National Park and the Wyoming Game and Fish Department have consistently agreed that 40% of the total annual harvest of the Jackson elk herd should be made in Grand Teton National Park (National Park Service, 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment, unpublished). That goal has never been achieved, not even when the harvests in the park and on the refuge are combined (Table 13). Since 1977, combined harvests from Grand Teton National Park and the National Elk Refuge have averaged 30.8%. Seven of 28 radio-collared elk harvested in Grand Teton National Park and the National Elk Refuge during this study summered outside Grand Teton National Park. Four of the seven were killed after 30 November when 80% of the Grand Teton National Park herd segment had already arrived at the refuge.

Two points are cogent. Hunting in Grand Teton National Park and the National Elk Refuge targeted the Grand Teton National Park herd segment after 1977. Hunting-season design altered the herd composition, but, based on estimated numbers of elk in the Grand Teton National Park valley, park and refuge hunts did not significantly change the size of the Grand Teton National Park herd segment (Tables 4 and 15).

Size and Composition of the Grand Teton National Park Herd Segment

The Grand Teton National Park herd segment increased substantially after the expansion of the park in 1950 and the removal of livestock from west of the Snake River in 1957 (Anderson 1958; Cole 1969; National Park Service, 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment, unpublished). Counts of the elk in the Grand Teton National Park central valley were initiated in 1963 to monitor the number of summering elk in the most accessible and most easily investigated area of the park. Based on these central valley counts, Boyce (1989) found an upward but statistically nonsignificant trend occurred between 1963 and 1985. Boyce (1989:49) evaluated the estimator for the central valley counts and noted that "due to differential (lower) visibility of mature males and the increased number of mature males in recent years, the total park population may have increased more since the mid-1960s than the trend counts indicate." We believe another source of bias is investigators' inability to detect any redistribution of elk from the relatively small area in the central valley where counts were conducted (about 90 km² or 8% of the land surface area of Grand Teton National Park) to adjacent lands as a function of density-dependent effects or human and environmental influences on the elk or their habitat.

Cole (1969) recognized that the central valley count area supported the highest densities of elk in Grand Teton National Park. He also noted that stochastic events, such as pine beetle control in 1965 and 1966, seemed to alter elk distributions with concomitant 40-50% reductions in the central valley count estimates of 1963. A steeper decline in 1986 resulted from poor census conditions (Table 4).

These same biases and high percentages of unclassified animals ($\bar{x} = 64 \pm 3.3\%$, $n = 16$; Table 4) could likewise result in the highly improbable male-to-female ratios during central valley counts.

The counts of elk in the central valley are not censuses of elk on lands east of State Highway 26/89/187 in Grand Teton National Park, on either side of Jackson Lake, along the Snake River riparian corridor, or north, south, and west of the inside Park Road (Moose to Jenny Lake to Jackson Lake; Fig. 1). Any changes in elk numbers in those areas would not be detected. Replicate counts by helicopter were initiated in 1990. They census elk in a larger area and should clarify the precision and accuracy of the valley count estimator (S. Cain and B. Smith, in preparation).

Cole's (1969) estimate of 2,800 elk in Grand Teton National Park during summer 1964 from a combination of ground, aerial, and track counts was the first attempt of a census in an area larger than the central valley of Grand Teton National Park. Houston (1968) estimated the size of the Grand Teton National Park herd segment as 3,250 during fall 1968.

The best direct count of the Grand Teton National Park herd segment was made in 1986. During an aerial survey on 12 November 1986, Wyoming Game and Fish Department biologists counted 685 elk along the west side of Jackson Lake and another 724 in the Grand Teton National Park valley. Back-tracking and track count data indicated that these were elk of the Grand Teton National Park herd segment. On the same day, 2,296 elk were counted and classified on the National Elk Refuge. These were primarily elk of the Grand Teton National Park herd segment because the earliest migrants to the National Elk Refuge are from Grand Teton National Park (Cole 1969; Smith 1985; this study). The total of 3,705 elk does not include remaining elk in the eastern portions of Grand Teton National Park or animals that had been harvested during the Grand Teton National Park and National Elk Refuge hunting seasons that opened on 25 October.

A corroborative estimate of the size of the Grand Teton National Park herd segment was derived from the summer distributions of the radio-collared elk. From 1978 to 1982, an average of 7,630 elk wintered on the National Elk Refuge. An average of 48.2% of the radio-collared elk or 3,678

(2,869–4,486, 95% CI) of the elk that wintered on the National Elk Refuge summered in Grand Teton National Park. Thus, the Grand Teton National Park herd segment composed one-third of the targeted number of elk in the Jackson herd unit (3,700 of 11,000 = 33.6%).

Throughout this study, removals of elk of the Grand Teton National Park herd segment during fall hunting seasons averaged 17%. Therefore, an estimated 4,460 (± 981 , 95% CI) elk summered in Grand Teton National Park prior to the fall harvests.

Population Regulation

Recruitment and Survival

Based on observed density-dependent recruitment, Boyce (1989) predicted that the number of elk in the Grand Teton National Park central valley (in the limited area where the valley count estimator is applied) would stabilize at about 2,000 animals in the absence of hunting. He discussed an experimental suspension of hunting in Grand Teton National Park as proposed in the Grand Teton National Park Natural Resources Management Plan (National Park Service, 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment, unpublished) to determine whether elk in the Grand Teton National Park valley would self-regulate their numbers.

Density-dependent regulation of ungulate populations is generally a function of the combined effects of environmental conditions and reduced forage quality and quantity on natality, survival, and dispersal (Sinclair 1977; Clutton-Brock et al. 1982). These effects are usually manifested in elk of the Rocky Mountain West during winter and spring months (Flook 1970; Craighead et al. 1973; Houston 1982).

Winter feeding has ameliorated the nutritional stress and limited over-winter mortality of elk to an average of 1.4% annually on the National Elk Refuge during the past 20 years (Boyce 1989; Smith and Wilbrecht 1990). Since 1960, the percentage of winter mortality has not correlated with the number of elk that wintered on the refuge ($r = -0.226$, $n = 28$, $P > 0.05$; Smith 1985). Boyce (1989) found evidence of density-dependent

recruitment among the elk that wintered on the National Elk Refuge in only 5 years since 1940 when he estimated feed-ground attendance by elk should have been highest because winter severity was greatest.

Free-ranging populations of large mammals generally respond in a density-dependent fashion to harvests that hold the populations below their ecological carrying capacity (Eberhardt 1977; Caughley 1979; McCullough 1984). Boyce (1989) attributed a significant increase in young-to-female-elk ratios after 1976 in Grand Teton National Park to an increased harvest of antlerless elk. Whether the source of the density-dependent recruitment was fecundity or survival of young were uncertain. Similar data for the other herd segments are not available.

Because of the nonlinearity in productivity curves of large mammals, the greatest density-dependent change among free-ranging populations is expected near carrying capacity (Fowler 1981). The relation between densities of elk in Grand Teton National Park and the ecological carrying capacity (K ; Caughley 1979) of these animals' summer range is unclear. Boyce (1989) asserted that harvests since the mid-1960s have kept the number of elk in the Grand Teton National Park central valley below K and possibly nearer a density that provides a maximum sustained yield. Given the ameliorating role of winter feeding on density effects in all herd segments, investigations of differences in fecundity, survival of young, and juvenile dispersal among the herd segments may clarify the role of density-dependence in the Jackson elk herd.

Dispersal

Dispersal can be an important regulating mechanism of populations that is most pronounced among males of polygynous mammals (Dobson 1982). At present densities, we found that adult radio-collared elk are not dispersing from Grand Teton National Park. Houston (1982) and Clutton-Brock et al. (1982) reported density-dependent recruitment and mortality but found little evidence of regulation by dispersal of high-density populations of elk and red deer that were not hunted.

Martinka (1969) found higher-than-expected numbers of yearling males and females in the Grand Teton National Park valley and on the

National Elk Refuge during some summers. He postulated that in some years a substantial fraction of yearlings do not migrate. The large number of yearlings that have summered in Grand Teton National Park and on the refuge since 1969 support Martinka's contention. The natal summer ranges of these nonmigratory yearlings is unknown. Failure to return to natal summer ranges outside Grand Teton National Park would add to the annual rate of increase of the Grand Teton National Park herd segment.

Restoration of Historic Distributions of Elk

The restoration of pre-1950 distributions and migrations of elk east of Grand Teton National Park remains an important objective of state and federal agencies because of the recreational, aesthetic, economic, and ecological benefits of conserving elk throughout all summer ranges in the national forest and the national parks. A significant decline in the number of elk migrating through the eastern portion of the Jackson herd unit since 1950 has been blamed on high harvest rates there (Boyce 1989). The lower harvest rates of radio-collared elk along eastern migration corridors offer encouragement that harvest strategies since 1978 may restore the elk of the eastern Yellowstone National Park and the Teton Wilderness herd segments to pre-1950 densities. Heavy antlerless harvests from 1977 to 1983 skewed sex ratios and probably dampened the growth rate of the Grand Teton National Park herd segment. But the overall size of that herd segment seemingly was not reduced. The emphasis on antlerless harvests was abandoned from 1984 to 1986. We predict that (1) in the absence of effective strategies to harvest elk that summer in and migrate through Grand Teton National Park, restoration of the pre-1950 distribution of elk in the Jackson herd unit will not occur and (2) the Grand Teton National Park herd segment will continue to compose at least half of the elk that winter on the National Elk Refuge.

We submit that experimental suspension of hunting in Grand Teton National Park, as proposed in the Grand Teton Natural Resource Management Plan (National Park Service, 1986. Grand Teton National Park Natural Resources

Management Plan and Environmental Assessment, unpublished), is a high-risk proposition. Once suspended, public sentiment may prohibit the reinstatement of hunting in Grand Teton National Park (Boyce 1989). Without a hunt in Grand Teton National Park, a burgeoning elk herd may require massive reductions by agency personnel on the National Elk Refuge. In 1935, refuge and state of Wyoming personnel culled 500 elk on the National Elk Refuge to help control herd size. This one-time cull was deemed unacceptable by the public. Extensive culling of elk by the National Park Service during the 1950s and 1960s was abandoned in 1969 as inappropriate management in Yellowstone National Park (Houston 1982).

Annual harvests on the National Elk Refuge have averaged about 30% of the combined Grand Teton National Park and refuge harvests (J. G. Griffin, 1985. Elk Hunting Plan National Elk Refuge. National Elk Refuge, unpublished). Without hunting on the National Elk Refuge and in Grand Teton National Park to remove elk of the Grand Teton National Park herd segment, the other herd segments require harvests that are higher than their annual rates of increase to hold numbers of elk on the refuge below 7,500. Alternatively, accepting larger numbers of elk on feed grounds would escalate economic and ecological costs that are contrary to sound resource stewardship.

One can argue that the humans' role in corrupting an evolved ecosystem has necessitated humans' role in manipulating the number of elk. The usurpation of historic winter ranges, removal of large predators, suppression of wildfire, establishment of the Yellowstone National Park and Grand Teton National Park ecological reserves in portions of the ecosystem, and selective modification of habitats outside those reserves through timber harvesting, road construction, and residential and agricultural encroachment have played a part in the legacy of Jackson Hole and its resilient elk herd. To mitigate these failings and maintain more than a remnant of the former herd, supplemental feeding was endorsed and institutionalized by the federal and state governments (Robbins et al. 1982). As an ironic consequence of its success, herd reductions through public hunts became necessary in Grand Teton National Park and on the National Elk Refuge.

To achieve Cole's (1969) third objective through herd removals will require changes in two areas of management: (1) establishing specific objectives for the spatial distribution of the number of elk on summer ranges; and (2) adopting new strategies to achieve elk removals that favor elk that summer in areas beyond Grand Teton National Park and that migrate east of Grand Teton National Park.

The other alternative is to terminate hunting on the National Elk Refuge and in Grand Teton National Park and test the hypothesis that density-dependent regulation stabilizes the Grand Teton National Park herd segment at or below its current size. A yield curve generated for elk that summer in the Grand Teton National Park central valley contains only one data point near the predicted K (Boyce 1989), which brings into question its reliability. More importantly, that model pertains only to a small part of the summer range of the Grand Teton National Park herd segment.

Predicting K is far from a precise science (Caughley 1976). In the absence of supplemental feeding, elk and other ungulate populations (Tanner 1966; Caughley 1970; Fowler 1981) periodically exceed K by a considerable margin as they oscillate in dynamic equilibrium with their environment. Rather than debate whether we can predict the carrying capacity of Grand Teton National Park and whether that number is acceptable for managing the Jackson elk herd in accordance with current policy constraints, we must first decide if human non-interference in ecological processes is appropriate and practical in Jackson Hole. By definition, natural regulation would require drastic reduction, if not elimination, of the supplemental winter feeding of elk. Cayot et al. (1979) correctly stated that natural regulation of elk populations is valid management in national parks with ecologically complete habitats. Presumptions about how or what may naturally regulate the elk population under prevailing conditions in Jackson Hole stretch the limits of ecological theory.

The elimination of hunting in Grand Teton National Park alone would not restore a naturally functioning ecosystem. Any lessons to be learned from the exercise would be confounded by other human interference and have questionable application elsewhere. Results from testing hypotheses

about natural regulation are probably inconclusive unless research is conducted in truly intact or restored ecosystems (Peek 1980).

Recommended Research

1. The accuracy and precision of classification counts of elk in the Grand Teton National Park valley should be verified by replication. Ongoing research (S. Cain and B. Smith, in preparation) indicates that the high male-to-female-elk ratios obtained from the central valley classification counts are inflated. Two factors bias those classifications: (1) the geographic area of the counts is perennially favored by males, and (2) the high percentage ($64 \pm 3.3\%$, $n = 16$) of unclassified animals that are largely female-young groups among all observed elk. Preliminary results indicate that counts from helicopters are superior to the traditional counts from the ground for estimating the herd size and composition.
2. After objectives for herd segments are established (see Management Recommendations), systematic aerial trend censuses should be implemented to monitor progress toward those objectives. Annual track counts enable wildlife managers to assess the relative numbers of elk that migrate from eastern and western portions of the Jackson herd unit. However, elk from two or three herd segments cross most track-count routes.
Previous aerial counts of elk on summer ranges did not account for visibility biases and were discontinued because of the variability of the results (Anderson 1958). Recently developed models for aerial winter counts of elk can correct inherent visibility biases (Samuel et al. 1987). Advancements in aerial census techniques and data analysis (Caughley 1974; Caughley et al. 1976; Samuel 1984) should be adopted to measure the sizes and compositions of herd segments in summer. The extensive forest fires of 1988 in Yellowstone National Park and in the Teton Wilderness should markedly improve the visibility of elk in formerly heavily forested areas.
3. Recruitment, survival, and dispersal of juvenile elk should be determined by capturing and

radio-tagging neonates in Grand Teton National Park and in the Bridger-Teton National Forest to investigate regulation of herd-segment sizes on summer ranges with high and low densities of elk. This research would address the premise for terminating the hunting of elk in Grand Teton National Park.

4. Results from the recommended studies should be incorporated into population-growth models for the Grand Teton National Park herd segment and, if possible, for the other herd segments. These models may help predict the outcomes of alternative management of the Jackson elk herd.

Recommended Management

Population Management

We offer four distinct options for the management of the Jackson elk herd on the assumptions that (1) the current objective of 11,000 wintering elk in the Jackson herd unit remains in effect, and (2) the responsible state and federal agencies continue to manage the herd for a variety of consumptive and nonconsumptive values.

Three options embrace the goal of restoring the pre-1950 distributions of elk in summer. That goal requires reducing the Grand Teton National Park herd segment by about half and concomitantly increasing the number of elk on national forest lands and in eastern Yellowstone National Park. Objectives for the desired size and age-sex composition of each herd segment would be established and would drive management decisions. The fourth option would not establish an objective for the size of the Grand Teton National Park herd segment.

Option 1. Refine current hunting regulations to achieve management objectives. Annual harvests of antlerless elk are necessary to restrain growth of the Grand Teton National Park herd segment. The opportunity to harvest elk of the Grand Teton National Park herd segment is influenced temporally by environmental conditions that initiate migration to the National Elk Refuge and by the increasing abundance of migrants from Yellowstone National Park and the Teton Wilderness in

Hunting Units 75, 76, 77, and 79 as the migration progresses. Offer the purchase of a second permit for antlerless elk to hunters in Hunting Unit 77 and possibly in Hunting Units 75 and 76 to increase harvests while elk of the Grand Teton National Park herd segment are migrating to the National Elk Refuge. Hunting seasons should close before 23 November in Hunting Unit 77 and before 1 December in Hunting Units 75, 76, and 79—earlier if targeted herd segments have passed through the areas and later only if elk migrations are greatly delayed by mild weather. Open the hunting seasons in Hunting Units 71, 79, and 81 on 1 October. Concurrent opening dates may disperse some elk from Grand Teton National Park east into adjacent national forest lands where they may be harvested.

To reduce harvests of elk in the eastern portion of the Jackson herd unit, move the opening of hunting season in Hunting Unit 70 from 10 September to 1 October. Close the hunting season in Hunting Unit 81 on 10 November to protect elk migrating to winter ranges in the Gros Ventre drainage and on the National Elk Refuge. Practices that enhance habitat effectiveness (Thomas 1979) for elk along migration corridors (including the maintenance of security cover and seasonal road closures) and on identified calving areas and winter ranges should receive high priority from land managers.

Option 2. Amend Public Law 787–81 to permit hunting in Grand Teton National Park west of the Snake River where most of the elk in Grand Teton National Park summer. Growth of the Grand Teton National Park herd segment has resulted from low winter mortality and inadequate harvests in the limited geographical areas in which elk can be hunted. Periodic harvests of elk west of the Snake River would achieve (1) sufficient harvests of elk of the Grand Teton National Park herd segment before they mingle with elk from other herd segments; (2) desired sex ratios of elk in Grand Teton National Park; (3) reduced harvest pressure, except when and if needed, on the elk of the Gros Ventre drainage, Teton Wilderness, and Yellowstone National Park herd segments that migrate to the National Elk Refuge by diminishing or eliminating the need for hunting in Hunting Units 75, 76, and 77; (4) harvests of elk in northwest Grand Teton National Park without reopening Hunting Unit 72 to hunting; and (5) improved

winter distributions and forage use by elk (reducing the need for artificial feeding) by closing or shortening the hunting seasons on potential winter range in Hunting Units 75–77. Although it is an ecologically rational approach to the elk management issue, this alternative will be unacceptable to members of the American public that object to hunting in national parks.

Option 3. Conduct periodic direct reductions of early migrants to the National Elk Refuge to reduce the Grand Teton National Park herd segment. Because the Jackson elk herd is infected with brucellosis, live elk cannot leave Teton County unless consigned for slaughter or first quarantined and tested for disease (Wyoming State statute 11-19-101; Legislative Service Office 1989). Suitable habitat elsewhere in the county is occupied, and the elk herds exceed desired numbers.

Direct reductions will elicit disapproval from the public. An alternative is the reduction or periodic elimination of winter-feed rations. Elk from all herd segments would suffer nutritional stress and increased mortality. This is contrary to current management policies of the National Elk Refuge and the Wyoming Game and Fish Department. Remotely delivered sterilants or abortifacients may offer a more humane alternative to direct reductions or deprivation of food.

Option 4. Experimentally terminate hunting in Grand Teton National Park and allow density-dependent factors to regulate the Grand Teton National Park herd segment. This is the preferred alternative in the Grand Teton National Park Resource Management Plan for management of elk (National Park Service, 1986. Grand Teton National Park Natural Resources Management Plan and Environmental Assessment, unpublished). Although this alternative is appealing, insufficient evidence suggests that the herd segment will decline or even stabilize at its present size with continuance of winter feeding on the National Elk Refuge.

In addition to these four alternatives, we see merit in management that requires more extreme departures from the current management philosophy. Winter feeding of elk should not be accepted as the necessary norm for the Jackson elk herd. It is costly, increases disease prevalence, and causes range damage (Thorne et al. 1979; Boyce 1989; Smith and Roffe 1994). Improving the distribution

of elk in winter throughout existing and potential winter ranges and substantially reducing winter feeding are worthy management goals. Ongoing range improvements (particularly prescribed burning, seeding and irrigation of refuge and forest rangelands, and reduction of livestock grazing on critical winter range in the Gros Ventre drainage) are collectively enhancing the carrying capacities for free-ranging elk. These practices, conservation easements, and acquisitions of available privately owned habitat are vital for a secure future of the Jackson elk herd. As these changes gradually shift winter distributions from the National Elk Refuge to winter ranges in the Bridger-Teton National Forest and in Grand Teton National Park, the proportion of elk of the Jackson elk herd that summer in Grand Teton National Park should decline.

This redistribution of elk in winter could be achieved without lowering the size of the Jackson elk herd below the current goal of 11,000 elk. About 14,000–15,000 elk are currently wintering in the Jackson herd unit and over 4,000 of those are not on feed grounds (D. Moody and T. Toman, Wyoming Game and Fish Department, personal communication, 1993). To formalize a change in the number of elk that are fed in winter, the state-federal agreement that endorses the maximum number of elk that winter on the National Elk Refuge should be changed from 7,500 to 5,500—as suggested by Murie (1951)—or fewer animals. One or more of the methods listed in management alternatives 1–3 are required to achieve an initial reduction to 5,500 or fewer wintering elk on the refuge. Required annual harvests and supplemental feeding will decline in future years as the number of elk that winter on the refuge declines.

Brucellosis Management

Long et al. (B. Long, M. Hinschberger, G. Roby, and J. Kimball, 1980. Gros Ventre cooperative elk study: final report 1974–1979. Wyoming Game and Fish Commission, Cheyenne. 192 pp.) advised delaying the initiation of grazing on calving areas until late June or July to avoid contact by cattle with elk fetuses and afterbirths. We agree and also recommend continued, resolute vaccination of young of all cattle in Teton and other counties with infected herds of elk and bison. Secondly, we

strongly discourage intentional and incidental feeding of elk or bison together with livestock. Thirdly, decreasing the dependence of the Jackson elk herd on supplemental feeding will reduce winter concentrations and disease transmission.

As an integral component of the greater Yellowstone area, the Jackson elk herd tests our commitment to the ideals of maintaining wild places and wild things. As a priceless slice of our wildlife heritage, the elk herd is a microcosm of the challenges elk—and people—will face throughout the coming years.

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Appendix A.

Duration of monitoring of 97 radio-collared elk (*Cervus elaphus*) of the Jackson elk herd, Wyoming, 1978–1984.

Year	Duration of monitoring (months)						Monitoring interval (days)		
	<i>N</i>	Range	$\bar{x}$	SE	<12 %	>24 %	Year	$\bar{x}$	SE
1978	24	0–32	13.3	1.9	41.7	8.3	1978	5.6	0.4
1979	17	1–14	5.3	1.1	94.1	0	1979	5.6	0.4
1980	29	0–60	32.4	3.5	17.2	62.1	1980	6.2	0.8
1981	21	6–48	22.0	3.2	19.0	33.3	1981	7.8	0.7
1982	6	2–36	15.2	6.3	66.7	33.3	1982	5.9	0.7
1978–79	41	0–32	9.4	1.3	64.4	4.9	1983	4.9	0.4
1980–82	56	0–60	27.3	2.4	21.3	48.2	1984	10.0	3.0
1978–82	97	0–60	19.2	1.6	40.2	29.9	1978–84	6.5	0.6

Appendix B.

Dosages of powdered succinyl-choline chloride used to immobilize elk (*Cervus elaphus*) at the National Elk Refuge, Wyoming, 1978–1983, and the duration of immobilization and recovery times of the elk.

Sex	N	Dosage (mg)	Immobilization time (min)	Recovery time (min)
		$\bar{x}$ SD (Range)	$\bar{x}$ SD (Range)	$\bar{x}$ SD (Range)
Male	19	22.9 ± 0.78 (22–24)	6.8 ± 2.85 (1–12)	38.4 ± 10.15 (22–60)
Female	40	21.1 ± 0.93 (20–23)	9.4 ± 5.42 (4–25)	37.3 ± 11.49 (16–54)
Total	59	21.7 ± 1.23 (20–24)	8.6 ± 4.84 (1–25)	37.7 ± 11.02 (16–60)

Appendix C.

Hunting regulations for the Jackson elk (*Cervus elaphus*) herd by hunting area, 1978–1986.^a

Area	1986	1985	1984
Area 70 Buffalo Fork Seasons	10 Sep–31 Oct: Mature males only	10 Sep–31 Oct: Mature males only 50 any-elk permits, spikes excluded	10 Sep–2 Nov: Antlered and 50 any-elk permits
Area 71 Pacific Creek Seasons	10 Sep–31 Oct: Mature males only 15 Oct–14 Nov: 100 any, spikes excluded	10 Sep–31 Oct: Mature males only 50 any permits, spikes excluded	10 Sep–11 Nov: Antlered and 50 any permits 27 Oct–11 Nov: 50 any permits
Area 72 Berry Creek	Closed	Closed	Closed
Area 74 Ditch Creek Seasons	Combined with Area 81	Combined with Area 81	Combined with Area 81
Area 75 Riverbottom Seasons	25 Oct–14 Nov: Any (permit only) 90 each week	26 Oct–15 Nov: Any (permit only) 90 each week	27 Oct–11 Nov: Any (permit only) 90 each week
Permits	270	270	270
Total Permits	270	270	270
Area 76 Blacktail/hayfields Seasons	25 Oct–14 Nov: Any (permit only) 160 a week of which 90 for only Blacktail Butte	26 Oct–15 Nov: Any (permit only) 160 a week of which 90 for only Blacktail Butte	27 Oct–11 Nov: Any by permit 160 a week of which 90 for only Blacktail Butte
Permits	480	480	480
Total Permits	480	480	480
Area 77 National Refuge Seasons	25 Oct–14 Nov: any (permit only) 120 week, maximum of 40 hunters at a time	26 Oct–15 Nov: Any (permit only) 120 each week, maximum of 40 hunters at a time	27 Oct–16 Nov: Any by permit 120 each week, maximum of 40 hunters at a time
Permits	360 any	360 any	360 any
Total Permits	360 any	360 any	360 any
Area 78 Wilson Seasons	Closed	Closed	15 Nov–15 Dec: Archery only
Area 79 Teton Park Seasons	25 Oct–14 Nov: Any (permit only) 1,500 any	26 Oct–15 Nov: Any (permit only) 1,000 any	27 Oct–11 Nov: Any (permit only) 1,000 any
Permit Type 1	None	None	10 Nov–11 Nov: 800 any
Permit Type 2	None	None	10 Sep–2 Nov: Antlered
Area 80 Sheep Creek Seasons	10 Sep–31 Oct: Mature males only	10 Sep–31 Oct: Mature males only	10 Sep–2 Nov: Antlered
Area 81 Spread Creek			

Appendix C. Continued.

Area	1986	1985	1984
Seasons	10 Sep-31 Oct: Mature males only & 100 antlerless permits	10 Sep-31 Oct: Mature males only & 100 any permits, spikes excluded	10 Sep-2 Nov: Antlered & 200 any permits
Area 82 Crystal Creek Seasons	10 Sep-31 Oct: Mature males only & 100 antlerless permits	10 Sep-31 Oct: Mature males only & 100 any permits, spikes excluded	10 Sep-2 Nov: Antlered & 200 any permits
Area 83 Fish Creek Seasons	1 Oct-31 Oct: Mature males only & 100 antlerless permits	1 Oct-31 Oct: Mature males only & 100 any permits, spikes excluded	1 Oct-31 Oct: Antlered & 200 any permits
Area	1983	1982	1981
Area 70 Buffalo Fork Seasons	10 Sep-15 Nov: Antlered 29 Oct-4 Nov: Any	10 Sep-29 Oct: Antlered 30 Oct-15 Nov: Any	10 Sep-30 Oct: Antlered 31 Oct-15 Nov: Any 16 Nov-06 Dec: Any in part of area
Area 71 Pacific Creek Seasons	10 Sep-28 Oct: Antlered 29 Oct-30 Nov: Any	10 Sep-29 Oct: Antlered 30 Oct-31 Dec: Any	10 Sep-30 Oct: Antlered 31 Oct-31 Dec: Any
Area 72 Berry Creek	Closed	Closed	Closed
Area 74 Ditch Creek Seasons	10 Sep-15 Nov: Antlered 24 Oct-04 Nov: Any	10 Sep-24 Oct: antlered 25 Oct-05 Dec: Antlerless	10 Sep-20 Oct: Antlered 21 Oct-06 Dec: Antlerless
Area 75 Riverbottom Seasons	29 Oct-30 Nov: 33 antlerless & 12 any permits at a time 45 permits per time period 170 any; 467 antlerless	30 Oct-05 Dec: 54 antlerless & 6 any permits at a time 60 permits per time period 95 any; 539 antlerless	31 Oct-06 Dec: 30 antlerless & 6 any permits at a time 36 permits per time period 95 any; 476 antlerless
Area 76 Blacktail/hayfields Seasons	29 Oct-30 Nov: Antlerless by permit only 135 a period (18 any) of which 60 are Blacktail Butte 255 any; 1,655 antlerless	30 Oct-05 Dec: Antlerless by permit only 150 a period (18 any) of which 60 are Blacktail Butte 95 any; 2,283 antlerless	31 Oct-06 Dec: Antlerless by permit only 72 a period (6 any) of which 36 are Blacktail Butte 95 any; 1,047 antlerless
Permits			
Total Permits			
Area 77 National Elk Refuge Seasons	29 Oct-30 Nov: 10 any & 30	30 Oct-05 Dec: Any until	31 Oct-06 Dec: Any until

Appendix C. Continued.

Area	1983	1982	1981
Permits	antlerless by permit only	migration, then antlerless only	migration, then antlerless only
Total Permits	120 a week, maximum 40 a day	150 a week, maximum 50 a day	120 a week, maximum 40 a day
Area 78 Wilson	320 any; 447 antlerless	385 any; 646 antlerless	596 any; 530 antlerless
Seasons	15 Nov-15 Dec: Archery only	15 Nov-05 Dec: Archery only	15 Nov-15 Dec: Antlerless
Area 79 Teton Park			
Seasons	29 Oct-30 Nov: Any (permit only)	30 Oct-05 Dec: Any (permit only)	31 Oct-06 Dec: Any (permit only)
Permit Type 1	1,500 any	1,500 any	1,500 any
Permit Type 2	12 Nov-30 Nov: 1,000 any	13 Nov-05 Dec: 1,500 any	14 Nov-06 Dec: 1,000 any
Area 80 Sheep Creek			
Seasons	10 Sep-04 Nov: Antlered	10 Sep-24 Oct: Antlered	10 Sep-20 Oct: Antlered
		25 Oct-10 Nov: Any	21 Oct-06 Nov: Any
		11 Nov-05 Dec: Antlerless,	07 Nov-06 Dec: Antlerless,
		noon opening	noon opening
Area 81 Spread Creek			
Seasons	10 Sep-31 Oct: Antlered	10 Sep-31 Oct: Antlered	10 Sep-20 Oct: Antlered
	24 Oct-04 Nov: Any	25 Oct-15 Nov: Any	21 Oct-15 Nov: Any
Area 82 Crystal Creek			
Seasons	10 Sep-31 Oct: Antlered	10 Sep-31 Oct: Antlered	10 Sep-31 Oct: Antlered
	10 Sep-15 Nov: 250 any permits	10 Sep-15 Nov: 300 any permits	01 Oct-15 Nov: 300 any permits
Area 83 Fish Creek			
Seasons	01 Oct-31 Oct: Antlered and	01 Oct-31 Oct: Antlered and	01 Oct-31 Oct: Antlered and
	300 any permits	350 any permits	300 any permits
Area	1980	1979	1978
Area 70 Buffalo Fork			
Seasons	20 Sep-17 Oct: Antlered	10 Sep-19 Oct: Antlered	10 Sep-20 Oct: Antlered
	18 Oct-15 Nov: Any	20 Oct-15 Nov: Any	21 Oct-15 Nov: Any
16 Nov-07 Dec: Any in 1-9 Dec: Any	part of area		
Area 71 Pacific Creek			
Seasons	10 Sep-17 Oct: Antlered	10 Sep-19 Oct: Antlered	10 Sep-20 Oct: Antlered
	18 Oct-31 Dec: Any	20 Oct-31 Dec: Any	21 Oct-31 Dec: Any
Area 72 Berry Creek			
	Closed	Closed	Closed
Area 74 Ditch Creek			
Seasons	10 Sep-17 Oct: Antlered	10 Sep-19 Oct: Antlered	10 Sep-20 Oct: Antlered
	18 Oct-17 Dec: Antlerless	20 Oct-09 Dec: Antlerless	21 Oct-03 Dec: Antlerless

Appendix C. Continued.

Area	1980	1979	1978
Area 75 Riverbottom Seasons	25 Oct-07 Dec: 25 antlerless & 5 any permits at a time 30 permits per time period 95 any; 471 antlerless	27 Oct-09 Dec: Antlerless by permit only 20 permits per week 251	28 Oct-03 Dec: Antlerless 20 permits per week 106
Permits Total Permits			
Area 76 Blacktail/hayfields Seasons	25 Oct-07 Dec: Antlerless by permit only 70 a period (10 any) of which 25 are Blacktail Butte 190 any; 1,131 antlerless	27 Oct-09 Dec: Antlerless by permit only 60 a week; 40 for hayfields; 20 for Blacktail Butte 503	28 Oct-03 Dec: Antlerless by permit only 60 a week; 40 for hayfields; 20 for Blacktail Butte 317
Permits Total Permits			
Area 77 National Refuge Seasons	25 Oct-07 Dec: any until migration; then only antlerless	20 Oct-02 Nov: Any 03 Nov-09 Dec: Antlerless by permit only	28 Oct-08 Dec: Antlerless by permit only
Permits Total Permits	120 a week; maximum of 40 a day 1,269 any; 280 Antlerless	120 a week; maximum of 40 a day 246 any; 778 Antlerless	120 a week; maximum of 40 a day 639 Antlerless
Area 78 Wilson Seasons	15 Nov-15 Dec: Antlerless	15 Nov-15 Dec: Antlerless	15 Nov-15 Dec: Antlerless
Area 79 Teton Park Seasons	25 Oct-07 Dec: Any by permit 1,500 Any	27 Oct-09 Dec: Any by permit 1,500 Any	28 Oct-03 Dec: Any by permit 1,500 Any
Permit Type 1	08 Nov-07 Dec: 1,000 Any	10 Nov-09 Dec: 1,000 Any	11 Nov-03 Dec: 1,000 Any
Permit Type 2	10 Sep-17 Oct: Antlered 18 Oct-31 Oct: Any	10 Sep-19 Oct: Antlered 20 Oct-02 Nov: Any	10 Sep-27 Oct: Antlered 28 Oct-08 Dec: Antlerless, noon opening
Area 80 Sheep Creek Seasons	01 Nov-07 Dec: Antlerless, noon opening	03 Nov-09 Dec: Antlerless, noon opening	
Area 81 Spread Creek Seasons	10 Sep-17 Oct: Antlered 18 Oct-15 Nov: Any 16 Nov-07 Dec: Antlerless in part of area	10 Sep-19 Oct: Antlered 20 Oct-15 Nov: Any 16 Nov-09 Dec: Antlerless	10 Sep-20 Oct: Antlered 21 Oct-15 Nov: Any 16 Nov-03 Dec: Antlerless
Area 82 Crystal Creek Seasons	10 Sep-15 Nov: Antlered 18 Oct-15 Nov: 300 Any permits	10 Sep-19 Oct: Antlered 20 Oct-15 Nov: 300 Any permits	10 Sep-20 Oct: Antlered 21 Oct-15 Nov: 300 Any permits
Area 83 Fish Creek Seasons	01 Oct-31 Oct: Antlered 18 Oct-15 Nov: 300 Any permits	01 Oct-14 Oct: Antlered 15 Oct-31 Oct: 250 Any permits	01 Oct-14 Oct: Antlered 15 Oct-31 Oct: 250 Any permits

^a See Fig. 3.

Appendix D.

Cattle allotments in the Bridger-Teton National Forest and Grand Teton National Park.

Allotment ^a	Number of cattle	Date in ^c	Date out ^c
Bridger-Teton National Forest			
A—Pacific Creek	249	6/1	8/22
B—Lava Creek East Unit	271	6/15	10/15
C—Lava Creek West Unit ^b			
D—Burro Hill	50	6/15	10/15
E—Fish Creek	1,959	6/11	10/15
F—Upper Gros Ventre	750	6/18	10/8
G—Redmond Creek	30	6/15	9/26
H—Taylor cattle and horse	15	5/15	11/15
I—Kinky Creek	174	6/11	10/15
J—Blackrock—Spread Creek	1,456	6/15	10/15
K—Ditch Creek	350	7/1	10/31
L—Miner's Creek	92	6/21	10/15
M—Bacon Creek	1,677	6/11	10/15
N—Big Cow Creek—Robinson	32	5/16	11/30
O—Bierer Creek	30	6/15	9/26
P—Breakneck	750	6/18	10/8
Grand Teton National Park			
Q—Gros Ventre pasture	1,200	5/15	6/15
R—Cunningham pasture	975	6/15	7/10
	975	10/15	11/15
S—Elk Ranch West	975	6/15	7/10
	975	10/15	11/15
T—Elk Ranch East	975	7/10	10/14
U—Sread Creek—Uhl	299	5/29	6/15
V—Pacific Creek	150	6/10	9/15

^a Figure 11 shows the location of the lettered allotments in the Jackson elk herd unit.

^b Used in alternate years with Lava Creek East and Burro Hill.

^c Grazing dates.

A list of current *Resource Publications* follows.

177. Field Manual for the Investigation of Fish Kills, by Fred P. Meyer and Lee A. Barclay, editors. 1990. 120 pp.
178. Section 404 and Alterations in the Platte River Basin of Colorado, by Douglas N. Gladwin, Mary E. Jennings, James E. Roelle, and Duane A. Asherin. 1992. 19 pp.
179. Hydrology of the Middle Rio Grande From Velarde to Elephant Butte Reservoir, New Mexico, by Thomas F. Bullard and Stephen G. Wells. 1992. 51 pp.
180. Waterfowl Production on the Woodworth Station in South-central North Dakota, 1965–1981, by Kenneth F. Higgins, Leo M. Kirsch, Albert T. Klett, and Harvey W. Miller. 1992. 79 pp.
181. Trends and Management of Wolf–Livestock Conflicts in Minnesota, by Steven H. Fritts, William J. Paul, L. David Mexch, and David P. Scott. 1992. 27 pp.
182. Selection of Prey by Walleyes in the Ohio Waters of the Central Basin of Lake Erie, 1985–1987, by David R. Wolfert and Michael T. Burr. 1992. 14 pp.
183. Effects of the Lampricide 3-Trifluoromethyl-4-Nitrophenol on the Pink Heelsplitter, by Terry D. Bills, Jeffrey J. Rach, Leif L. Marking, and George E. Howe. 1992. 7 pp.
184. Methods for Detoxifying the Lampricide 3-Trifluoromethyl-4-Nitrophenol in a Stream, by Philip A. Gilderhus, Terry D. Bills, and David A. Johnson. 1992. 5 pp.
185. Group Decision-making Techniques for Natural Resource Management Applications, by Beth A. Coughlan and Carl L. Armour. 1992. 55 pp.
186. DUCKDATA: A Bibliographic Data Base for North American Waterfowl (Anatidae) and Their Wetland Habitats, by Kenneth J. Reinecke and Don Delnicki. 1992. 7 pp.
187. Dusky Canada Goose: An Annotated Bibliography, by Bruce H. Campbell and John E. Cornely. 1992. 30 pp.
188. Human Disturbances of Waterfowl: An Annotated Bibliography, by Robert B. Dahlgren and Carl E. Korshgen. 1992. 62 pp.
189. Opportunities to Protect Instream Flows and Wetland Uses of Water in Nevada, by James L. Bingham and George A. Gould. 1992. 33 pp.
190. Assessment of Habitat of Wildlife Communities on the Snake River, Jackson, Wyoming, by Richard L. Schroeder and Arthur W. Allen. 1992. 21 pp.
191. Evaluating Temperature Regimes for Protection of Smallmouth Bass, by Carl L. Armour. 1993. 26 pp.
192. Sensitivity of Juvenile Striped Bass to Chemicals Used in Aquaculture, by Terry D. Bills, Leif L. Marking, and George E. Howe. 1993. 11 pp.
193. Introduction of Foxes to Alaskan Islands—History, Effects on Avifauna, and Eradication, by Edgar P. Bailey. 1993. 53 pp.
194. Distribution and Abundance of Predators that Affect Duck Production—Prairie Pothole Region, by Alan B. Sargeant, Raymond J. Greenwood, Marsha A. Sovada, and Terry L. Shaffer. 1993. 96 pp.
195. Evaluating Temperature Regimes for Protection of Walleye, by Carl L. Armour. 1993. 22 pp.
196. Evaluation of Five Anesthetics on Striped Bass, by Carol A. Lemm. 1993. 10 pp.
197. Standardization of Roadside Counts of Columbids in Puerto Rico and on Vieques Island, by Frank F. Rivera-Milán. 1993. 26 pp.
198. Herpetofaunal Diversity of the Four Holes Swamp, South Carolina, by Russell J. Hall. 1994. 43 pp.



U.S. DEPARTMENT OF THE INTERIOR NATIONAL BIOLOGICAL SURVEY

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