

Migratory Behavior of Hunted Elk

Abstract

During 1990–2000, I investigated patterns of fall migration and harvests of the Jackson elk herd. Specifically, I compared the timing of fall migration of the 2,500–4,500 elk (*Cervus elaphus*) that summered in Grand Teton National Park (GTNP) and wintered on the National Elk Refuge (NER) with elk that used other summer ranges by monitoring 512 migrations of radiocollared elk and by direct counts of elk arriving at the NER. Annual timing of migrations of GTNP elk was related positively to herbaceous standing crop ($r^2 = 0.89$) and residual standing crop (forage remaining at the end of the summer-fall grazing season, $r^2 = 0.82$) in GTNP. The number of elk on the NER the previous winter accounted for 39% of the residual variation in migration timing. Migrations of elk from higher elevation summer ranges were inversely related to cumulative snowfall through 10 November each fall, whereas elk from GTNP initiated migrations when snow depths averaged <2 cm. Vegetation offtake averaged 62% in GTNP when elk migrated to access superior foraging areas in the NER. Counter-intuitively, early migration of GTNP elk from their national park sanctuary, through a migratory corridor where they were heavily hunted, may be adaptive. Early migrants from GTNP to the NER experienced 4.8% harvest compared to 11.3% harvest ($P = 0.037$) of elk migrating after the median migration date each fall. Combined harvest and winter mortality rates were lower among early migrants ($P < 0.01$). I describe how early migration behavior may be selected over time. Such behavioral adaptation on elk ranges encompassing sanctuaries from hunter harvest challenge wildlife managers' skillfulness to manage elk numbers across heterogeneous topographic and jurisdictional landscapes.

Introduction

Migration is an adaptive behavioral strategy that evolved to avoid resource bottlenecks in temperate regions (McCullough 1985). Migration can enhance fitness by increasing survival and reproduction (Dingle 1985). Migrants have access to greater food supplies due to their larger ranges, and access to optimum phenological stages or patches of forage. Migrants may also be less vulnerable to predators, which tend to be territorial and therefore do not follow migratory herds throughout their ranges. Indeed, migratory species of ungulates inhabiting strongly seasonal environments may outnumber non-migratory species by an order of magnitude (Fryxell et al. 1988).

Like most populations of elk (*Cervus elaphus*) in western North America, the Jackson elk herd of northwest Wyoming is migratory, traveling 10–100 km between seasonal ranges. Summer distribution was described by Cole (1969) and Smith and Robbins (1994) as 4 relatively distinct units referred to as herd segments: Grand Teton National Park (GTNP), southern Yellowstone National Park (YNP), the Teton Wilderness Area (TW), and the Gros Ventre drainage (GV) (Figure

1). Adult elk displayed high fidelity to herd segments but commingled during migration and on winter ranges (Cole 1969, Smith and Robbins 1994, Smith and Anderson 2001).

Since 1960, the State and federal agencies that cooperatively manage the Jackson elk herd have strived to reduce the number of elk that summered in and migrated through Grand Teton National Park (GTNP) to the National Elk Refuge (NER) as a proportion of the Jackson elk herd (Cole 1969, Boyce 1989, Smith and Robbins 1994). Public elk hunts in parts of GTNP and the NER, where 60% of the Jackson elk herd and virtually all GTNP elk are supplementally fed in winter, are controversial but considered crucial to controlling elk numbers (Boyce 1989). Eighty to 95% of annual mortality of elk >1-year-old results from hunter harvest (Smith and Robbins 1994, Smith and Anderson 1998). Yet the Jackson herd has exceeded the state of Wyoming's population objective of 11,029 elk in all but 2 years since 1980 (Lubow and Smith 2004). Boyce (1989) and Smith and Robbins (1994) correlated spatial variation of elk harvests with vulnerability of elk on different summer ranges and migration routes. They inferred that increasing numbers of elk summering in GTNP from the 1950s through 1980s resulted from lower harvests of these elk than elk from national forest summer ranges. Differences in recruitment and

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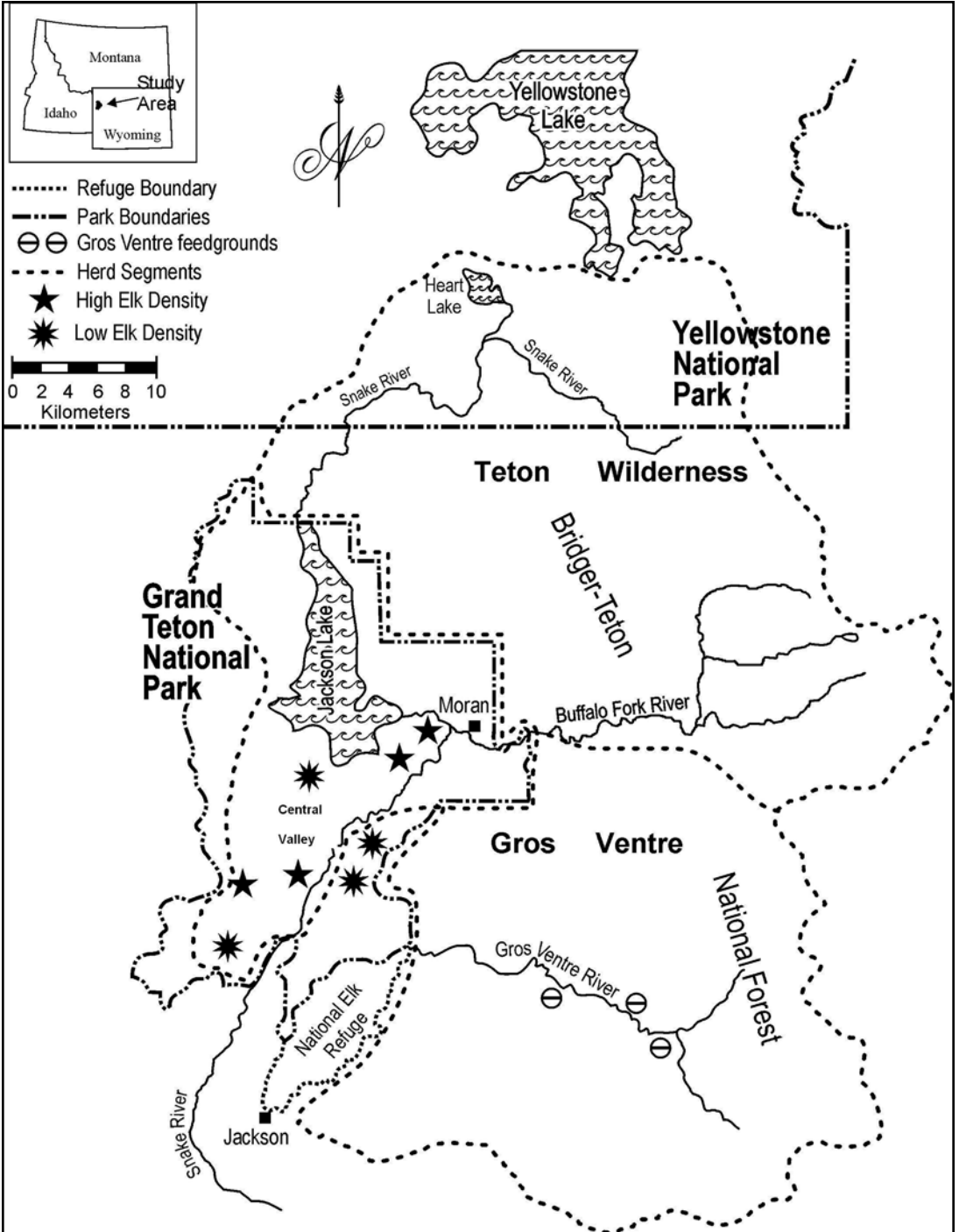


Figure 1. Summer herd segment boundaries of the Jackson elk herd: Grand Teton National Park, Yellowstone National Park, Teton Wilderness, and the Gros Ventre drainage and locations of vegetation sampling in areas of high (★) and low (⊛) elk densities.

dispersal among summer ranges apparently do not account for the increase in GTNP elk (Smith and Anderson 1996, 2001).

Fall migrations of the Jackson herd have been studied since 1945 based on counts of tracks in the snow, fixed-wing observations of migrating elk, counts of elk arriving at winter ranges (Murie 1951, Anderson 1958, Cole 1969, Boyce 1991), and by radio-telemetry (Smith and Robbins 1994). Timing of fall migrations of elk from high elevation summer ranges in the Teton Wilderness Area (TW) and Yellowstone National Park (YNP)(Figure 1) correlated with fall snow accumulations (Smith and Robbins 1994), which Boyce (1991) considered an adaptive response to diminishing forage availability as snow accumulated on summer ranges. Contrarily, migrations of elk from the lower elevation summer ranges of GTNP appeared unrelated to snow depths, and often preceded significant snow accumulations. This migratory behavior is particularly perplexing because GTNP elk leave areas free of hunting and traverse areas which are heavily hunted.

Given the complexities of harvesting elk and the NER's winter feeding program, which limits winter mortality (Smith and Anderson 1998), controlling the size of the Jackson herd, particularly those that summer in national parks, has proven challenging (Boyce 1989, Smith and Robbins 1994, Lubow and Smith 2004). To design hunting seasons that achieve sufficient harvests of elk that are summer resident in national park sanctuaries, wildlife managers need to know the routes that elk travel between various summer and winter ranges, and what factors initiate fall migrations. Here I examine factors correlated with annual timing of migrations from GTNP and other summer ranges and associated survival patterns of elk.

I hypothesized that migration from high elevation summer ranges in TW and YNP occurred when snowfall limited access to food. Conversely, I hypothesized that migration from GTNP correlated with annual vegetation production or utilization rates by mid-autumn, and possibly elk densities. Consequently, GTNP elk would migrate from relatively snow-free areas closed to hunting and through areas open to hunting to optimize their fall diets at the NER winter range, which is ungrazed and partially irrigated during the growing season to promote favorable winter foraging.

I also hypothesized that early migrants from GTNP would experience similar or greater survival during the hunting season and/or during winter than elk that migrated after the median date of migration. If early migration enhanced survival, it could be considered adaptive behavior and favored through selection. Given that elk from all herd segments were hunted and supplementally fed on the NER, I hypothesized that fall and winter survival would not differ between migrants from GTNP and elk using other summer ranges.

Data on these topics would help wildlife managers determine whether efforts to equitably harvest elk from all herd segments have been effective, and how harvest strategies may be refined. They are also of interest to ecologists and evolutionary biologists seeking the derivation of incipient migratory behavior (Cox 1968, Sinclair 1983, Dingle 1985), and to the public which owns and values these resources.

Study Area

Cole (1969), Boyce (1989), and Smith and Robbins (1994) described the boundaries, topography and vegetative communities of the Jackson elk herd's range. Elevation ranges from 1,950 to 3,650 m. Mean annual temperatures decrease, and precipitation and snowfall increase from the NER northward to YNP (Smith and Robbins 1994). At Moran, in the center of the study area at 2,069 masl mean annual precipitation was 639 mm (Figure 1). January and July monthly temperatures averaged -9.7 C and 15.7 C, respectively (National Oceanic and Atmospheric Administration 2005). Further north at the south entrance of Yellowstone National Park (elevation 2,098 masl), annual precipitation averaged 678 mm and January and July temperatures averaged -11.2 C and 13.5 C, respectively.

During 1990–2000, about 70% of the estimated 14,000–18,000 Jackson elk herd was supplementally fed each winter (Lubow and Smith 2004). At the NER, an average $8,460 \pm 444$ elk were fed alfalfa hay for 65 ± 6.5 days each winter. Nearly all the elk that summer in GTNP winter on or adjacent to the NER, whereas elk from the other 3 herd segments winter at three State of Wyoming feedgrounds in the Gros Ventre drainage, free-range on the Bridger-Teton National Forest and GTNP lands north of the NER, or winter on and adjacent to the NER (Figure 1). About half the elk that wintered on the NER summered in

GTNP, 40% in YNP and TW, and the remainder in the GV herd segment during the 1980s (Smith and Robbins 1994).

During the 1980s, about 4,500 elk spent each summer in GTNP, largely in the western three-fourths of the park closed to hunting (Smith and Robbins 1994). Elk numbers within the Central Valley of GTNP (Figure 1) averaged 5.9 elk/km² compared to 2.4 elk/km² outside GTNP in 1991 (Smith and Anderson 2001). An additional 2,000–3,000 elk that summered in the western half of the TW and YNP migrated through the Central Valley of GTNP en route to the NER. Those migrant elk and the elk of GTNP traversed Hunt Units 75-77 of eastern GTNP and the NER to reach winter range on the NER (Smith and Robbins 1994). The southern half of the NER was closed to hunting. All hunting units, except Hunt Unit 72, were open to elk hunting during this study (Figure 2).

Methods

Captures

I captured and radio-monitored elk that summered in each of the 4 summer herd segments of the Jackson Elk Herd. During 1990–1992, 167 newborn elk were captured and equipped with expandable radiocollars within a week of birth (\bar{x} = 3.6 ± 0.19 days, Smith et al. 1998). I used a stratified random sampling design of two groups of 25 elk neonates/yr: one group that would summer inside GTNP and another group that would summer outside the park (Smith and Anderson 1996). Most of the elk that frequent calving areas where I captured neonates winter on or adjacent to the NER (Smith and Robbins 1994). During February and March 1992–1994, I recaptured 50 of these elk (now 0.7–2.8 years old) with thiafentanil administered via dart gun (Smith et al. 1998) and replaced their radiocollars with non-expanding radiocollars manufactured by Telonics Inc. (Mesa, Arizona). I supplemented this sample of instrumented elk by darting 43 yearling females on the NER during February and March 1994–1997.

I captured another 154 neonates during 1997–1999 and equipped each with a radio transmitter eartag (Smith et al. 2006). During February and March 1998–2000, I recaptured 36 of those calf elk on the NER, fitted them with non-expanding

radiocollars, and documented their distributions and migrations in subsequent years. I followed animal welfare protocol as outlined by the University of Wyoming and the U.S. Fish and Wildlife Service at the time of the study (Title 9 Code of Federal Regulations, Chapter 1, Subchapter A, Section 2.31).

Monitoring Elk Distribution and Migration

From 2 data sets I documented chronology of fall migrations. As elk from the 4 herd segments arrived on the NER each fall, they congregated on the grasslands and marshlands comprising the southern 40% of the NER closed to hunting. Using binoculars and spotting scopes, I counted the elk approximately 3 times weekly from adjacent hillsides. Each February, agency personnel from feed wagons counted all elk being fed on the NER (Smith and McDonald 2002). I used the date on which half of each winter count had arrived at the refuge during my previous fall counts to represent the median migration date of the wintering population during 1982–2000.

Secondly, I indexed migration of each of the 4 summer herd segments from movements of the radiocollared elk (Figure 1). During summer through mid-October 1990–1992, I located radioed elk three times weekly from ground stations or 2–3 times weekly from aircraft. I located elk at least 3 times weekly during fall migrations (Smith and Anderson 1998). Beginning mid-October, I recorded arrival of elk at the NER by monitoring telemetry signals 5 times/week with hand-held antennas from hillsides adjacent the NER. Thus, I was able to calculate departure dates of elk from summer ranges (first location of an elk beyond its summer range en route to winter range), arrival at winter ranges, duration of staging in GTNP's Central Valley (Figure 1), and duration of migrations. I defined staging as an interruption or slowing of migration progress that occurred once an animal entered the Central Valley of GTNP and until it entered hunting units 75-77 en route to NER winter range. This winter range included the refuge and national forest lands immediately east of the NER. After 1992, I monitored arrival of elk at the NER as in previous years. However, I did not determine departures from summer ranges and time spent migrating and staging along migration routes because transmitter relocations beyond the NER were obtained only weekly or biweekly.

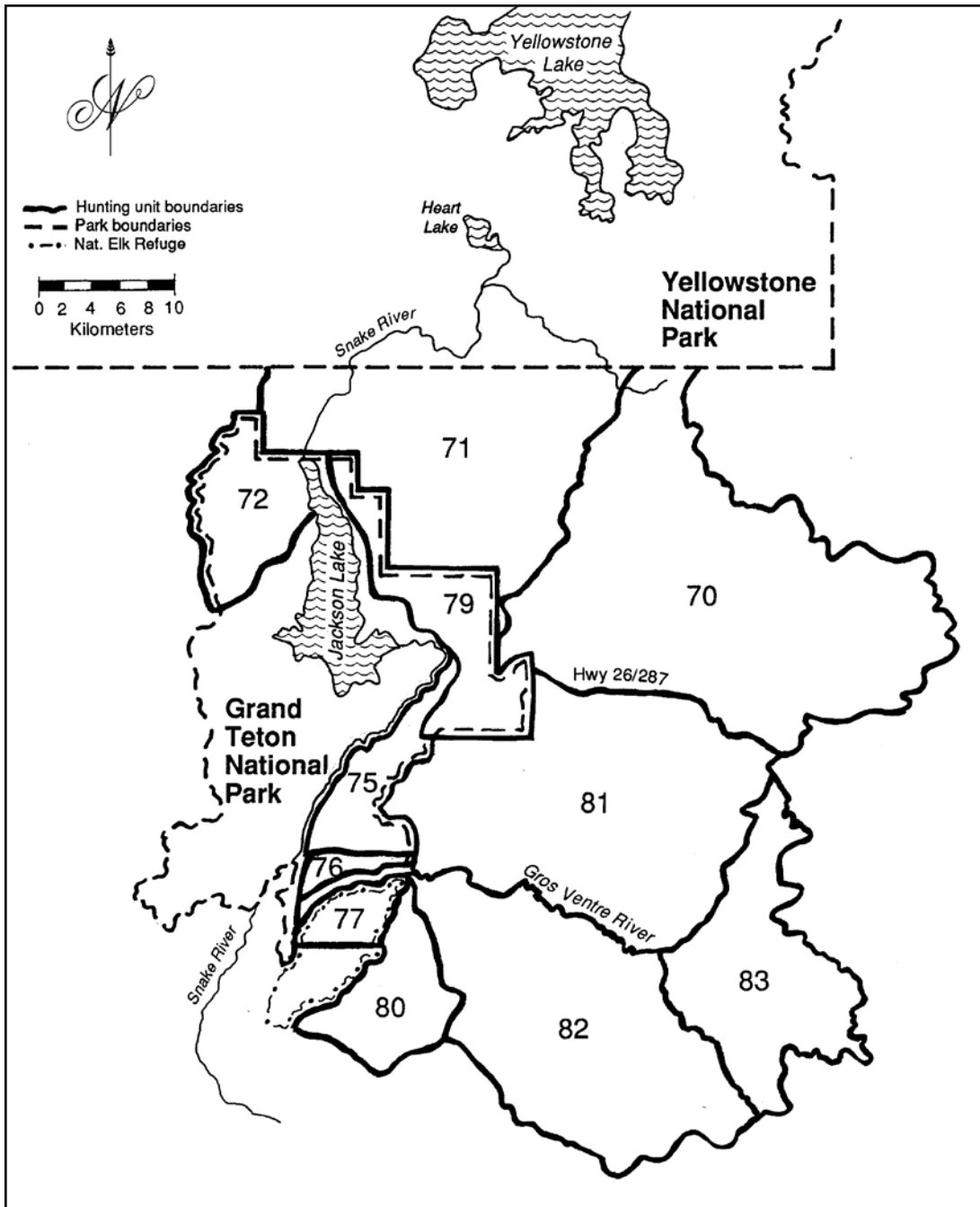


Figure 2. Hunting unit boundaries of the Jackson elk herd. All areas of west of Jackson Lake and the Snake River (including Unit 72), Yellowstone National Park, and the south half of the National Elk Refuge were closed to elk hunting.

I compared duration and timing, and correlates with these, of migrations of GTNP elk to elk of

TW and YNP combined (designated TW-YNP). The sample contained too few elk from the Gros

Ventre herd segment for most comparisons without a high probability of Type II statistical error. Migratory behavior can vary between the sexes, with males migrating in advance of female-calf groups (Irwin 2002). To test for such an effect within my data set, I compared mean arrival dates at the NER of all calves and older females to all 1+ year-old males. Finding no such main effect ($F_1 = 0.16, P = 0.69$) nor a two-way interaction of gender with summer range (GTNP vs. TW-YNP summer range, $F_1 = 0.003, P = 0.96$), I analyzed migratory behavior for the sexes combined.

Harvest Statistics

Fates of radiocollared animals provided comparisons of hunting mortality among herd segments. Hunters were cooperative in reporting harvests of radioed elk as per information embossed on radiocollars. I combined unretrieved, hunter-crippled animals that I found dead with legally and illegally hunter-killed elk as harvested animals. Harvest rates of radioed elk that were killed in Hunt Units 75–77 and 80 during migration to the NER (Figure 2) are presented as the proportion of those migrating that were killed. Elk that summered and were harvested in Hunt Unit 79 before migrating were excluded from the sample.

The proportion of early GTNP migrants to the NER that were harvested en route was compared to the proportion harvested from GTNP migrants arriving after the median arrival date. I also compared proportions of early migrants to late migrants that died during winter.

Forage Sampling

I measured net primary production and its utilization in portions of GTNP to relate timing of fall migrations to annual vegetation abundance and depletion. During each spring of 1992–1998, I clipped the previous year's standing crop at 8 locations in GTNP. The experimental design stratified the Central Valley of GTNP into two areas: one in which high densities of elk were known to occur during summer and fall and the other area where relatively lower densities of elk occurred (Smith and Robbins 1994, Anderson et al. 1998). Where vegetation was sampled, elk were by far the most abundant large grazer (Grand Teton National Park 1996). I further stratified each of those areas by dominant plant community type and soil type (Soil Conservation Service 1982). Four locations in the area of high elk densities were thus matched to 4 locations in the area of relatively low elk densities (Table 1, Figure 1). Herbaceous vegetation in the plant communities sampled consisted of native grasses and forbs at range sites rated in fair to good condition.

At each of the 8 locations, 3 sampling sites were chosen. The first site was located at the Universal Transverse Mercator system coordinates of the randomly selected location. The second site was 30 m due north of the first. The third site was 30 m southeast of the second (Figure 3). At each site I ocularly chose two 1-m² spots with similar forage production and composition within 10 m of each other. By the flip of a coin, one was protected with a 1-m-diameter exclosure, constructed of welded

TABLE 1. The random sampling design (see Figure 3), stratified by relative elk densities, soil type, and plant community type, employed to measure herbaceous standing crop and offtake at 8 locations (Figure 1) in Grand Teton National Park, 1991–1997. Results represent the 7-year mean \pm SE in grams/meter².

Elk density	Plant community	Soil type	Ungrazed plots ¹	Grazed plots ²	% offtake
High	Sagebrush-grassland (north)	Tineman-Bearmouth	9.0 \pm 0.9	3.9 \pm 0.4	57
High	Sagebrush-grassland (south)	Tineman-Bearmouth	11.6 \pm 1.4	5.0 \pm 0.7	57
High	Coniferous forest	Turnerville	19.9 \pm 1.9	5.6 \pm 0.6	72
High	Aspen woodland	Taglake-Sebud	22.1 \pm 2.3	9.0 \pm 1.5	59
Low	Sagebrush-grassland (north)	Tineman-Bearmouth	7.0 \pm 0.8	6.3 \pm 0.7	10
Low	Sagebrush-grassland (south)	Tineman-Bearmouth	7.4 \pm 0.6	6.0 \pm 0.6	19
Low	Coniferous forest	Turnerville	9.0 \pm 1.0	7.7 \pm 0.6	14
Low	Aspen woodland	Taglake-Sebud	12.4 \pm 1.0	9.1 \pm 0.9	27

¹ A total of 12 plots were clipped at each of the 8 locations—4 beneath each of the 3 exclosures.

² A total of 12 plots were clipped at each of the 8 locations—4 at each of the 3 unprotected paired sites.

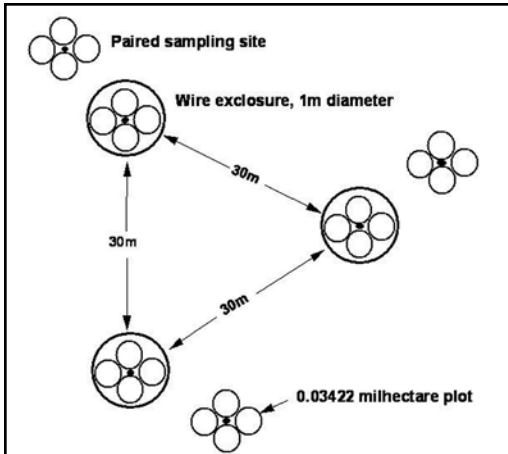


Figure 3. Experimental design of the standing crop sampling conducted at each of 8 locations in Grand Teton National Park.

wire reinforced with 1-cm-diameter rebar, and one was not protected. I permanently marked the centers of both spots with a steel pin.

Each spring, immediately after snow melted from the 8 sampling locations, I clipped and bagged the previous year's standing crop from four 0.3422-m² circular plots within each of the 1-m² spots (Figure 3). Thus, vegetation from a total of 192 plots was clipped each spring. After air-drying, I weighed the vegetation from each plot to the nearest 0.5 g. Weights from the 4 plots beneath each enclosure were averaged as they were on the 4 plots from each paired, grazed site. I used the herbaceous vegetation I clipped from plots protected by enclosures as estimates of the previous year's "standing crop," roughly equivalent to net above ground primary production. The vegetation remaining on plots that were not protected by enclosures estimated "residual standing crop." The difference between the two constituted the amount of vegetation utilized by large herbivores.

Based on findings during 1992–1998, residual standing crop from the 4 sampling locations of high elk densities proved sufficient ($r^2 = 0.82$) to correlate forage conditions with weather conditions and with timing of elk migrations from GTNP. Therefore, I sampled only residual standing crop from the 4 high elk density locations during 1999–2001 to reduce sampling effort. Given concerns about the influence of enclosures on

forage production (Owensby 1969), relying on measurements of residual standing crop from unprotected plots avoided potential biases.

Statistical Treatment

To examine relationships between the timing of fall migrations and various environmental variables, I used least squares linear and step-wise multiple regression. I analyzed vegetation data as a three-way factorial ANOVA design with year, elk densities, and whether or not plots were grazed as the grouping factors. Herbaceous standing crop was the dependent variable. I modeled annual net primary production using backward stepwise multiple regression. Independent variables included monthly precipitation totals and mean monthly temperatures during each growing season month, May–July.

I used likelihood ratio chi-square and Fishers' exact tests to analyze goodness of fit of categorical data including differences in harvest rates between the sexes, between summer ranges, and between early and late migrating elk to the NER. I used SYSTAT 10.2 (SYSTAT, Inc., Evanston, Illinois) statistical software package for all analyses. For all statistical tests, $\alpha < 0.05$ was considered significant. Means are presented \pm standard errors.

Results

Duration of Fall Migrations

Fall migrations commenced in October or early November. Although departure of elk from summer ranges during 1990–1992 did not differ among the four herd segments, the duration of fall migrations varied with the distance between summer ranges and the NER (Table 2). The GTNP herd segment spent significantly less time in migration than all others.

Prior to crossing the Snake River en route to the NER, many of the 2,500–4,500 elk that summered in GTNP plus 2,000–3,000 elk from TW and YNP gathered and foraged in late October and November each fall in the Central Valley of GTNP (Figure 1). During 1990–1992, elk that summered in GTNP spent 72% ($\bar{x} = 4.2 \pm 0.8$ days) of their migration time ($\bar{x} = 5.8 \pm 0.7$ days) staging. By contrast, radio-collared elk from the TW–YNP herd segments that migrated through GTNP on their way to the NER, spent 28% of their migration time staging (\bar{x} migration time =

TABLE 2. Departures of radio-collared elk from summer ranges and duration of migrations from Yellowstone National Park (YNP), Teton Wilderness Area (TW), the Gros Ventre drainage (GV), and Grand Teton National Park (GTNP) to winter range on and adjacent to the National Elk Refuge, 1990–1992. Differences among summer ranges were tested with one-way ANOVA and Tukey’s post-hoc pairwise comparisons

Summer range	Departure (Julian date)			Summer range (test result)				Migration time (days)			Summer range (test result)			
	<i>n</i>	\bar{x}	SE	GTNP	GV	TW	YNP	<i>n</i>	\bar{x}	SE	GTNP	GV	TW	YNP
GTNP	106	301	1.0	–	NSD	NSD	NSD	101	5.8	0.7	–	**	**	**
GV	11	303	5.4		–	NSD	NSD	8	18.4	5.7		–	*	NSD
TW	10	301	7.6			–	NSD	4	33.5	3.7			–	NSD
YNP	22	302	2.8				–	16	27.1	4.3				–

* = $P < 0.05$; ** = $P < 0.01$; NSD = no significant difference

27 ± 3.4 days, \bar{x} staging time = 7.5 ± 2.4 days). Migrations of TW–YNP elk that migrated through GTNP west of the Snake River ($n = 16$) averaged 24.4 ± 3.7 days to reach the NER, compared to 44 ± 3.7 days for TW–YNP elk ($n = 4$) that migrated east of the Snake River ($t_1 = 2.5$, $P = 0.02$).

Arrival at the National Elk Refuge

The mean annual arrival dates of radio-collared elk correlated ($r^2 = 0.97$, $F_{1,9} = 332$, $P < 0.001$) with arrival of 50% of the entire herd that wintered at the NER, suggesting that migrations of this sample of radioed animals were representative of the elk population. Mean arrival dates of radioed elk at the NER varied annually for GTNP elk ($F_{10,369} = 55.6$, $P < 0.001$), and also for elk that summered

in TW–YNP ($F_{10,114} = 11.8$, $P < 0.001$), and the GV ($F_{9,21} = 2.7$, $P < 0.03$).

Radioed elk that summered in GTNP arrived 6–31 days ($\bar{x} = 16.4 \pm 7.7$) earlier at the NER each year than elk from TW–YNP (Table 3). Elk that summered in areas of GTNP closed to hunting ($n = 324$) arrived no earlier at the NER than elk that summered in areas of GTNP open to hunting (Unit 79; $n = 49$) during 1990–2000 ($t_{371} = 0.27$, $P = 0.79$). However, elk departed summer ranges in Hunting Unit 79 (Figure 2) sooner ($t_{104} = 2.4$, $P < 0.02$) and spent an average 9 more days migrating to the NER ($t_{99} = 4.0$, $P < 0.001$) than did elk that summered in areas of GTNP closed to hunting. These earlier departures appeared related to the opening of the annual hunting season in Unit 79

TABLE 3. Migrations of radioed elk from Grand Teton National Park (GTNP), and from the Teton Wilderness Area and Yellowstone National Park (TW–YNP) herd segments in relation to hunting season dates in Hunt Units 75–77. Student’s *t* tests compare mean arrival dates of GTNP and TW–YNP elk at the National Elk Refuge.

Year	Hunting season		No. of radioed elk arriving after hunting season ends		Mean arrival date at the National Elk Refuge				Test result
	Began	Ended	GTNP	TW–YNP	GTNP		TW–YNP		
1990	20 Oct	30 Nov	0 of 28	2 of 5	309	5 Nov	321	17 Nov	<0.002
1991	12 Oct	29 Nov	0 of 36	3 of 12	305	1 Nov	321	17 Nov	<0.001
1992	10 Oct	30 Nov	0 of 51	1 of 5	306	2 Nov	337	2 Dec	<0.001
1993	9 Oct	30 Nov	5 of 27	11 of 13	330	26 Nov	353	19 Dec	<0.001
1994	8 Oct	4 Dec	0 of 33	0 of 13	303	30 Oct	315	11 Nov	<0.001
1995	7 Oct	3 Dec	0 of 29	0 of 12	314	10 Nov	320	16 Nov	<0.002
1996	5 Oct	6 Dec	0 of 34	0 of 17	311	6 Nov	322	17 Nov	=0.005
1997	11 Oct	14 Dec	0 of 32	1 of 12	321	17 Nov	332	28 Nov	=0.003
1998	17 Oct	13 Dec	2 of 31	1 of 13	328	24 Nov	339	5 Dec	=0.019
1999	16 Oct	12 Dec	8 of 37	12 of 15	340	6 Dec	358	24 Dec	<0.001
2000	14 Oct	10 Dec	0 of 38	9 of 15	324	19 Nov	351	16 Dec	<0.001
Total			15 of 376	40 of 132	317	13 Nov	334	30 Nov	<0.001

(Table 3), and the additional migration time was spent in GTNP's Central Valley. Mean arrival of TW–YNP elk that migrated west of the Snake River was 28 November compared to 11 December for TW–YNP elk that migrated east of the Snake River ($t_{114} = 2.6, P = 0.01$).

Vegetation Production and Utilization

For the 7 years I sampled vegetation on all 192 plots, I found a significant two-way interaction between elk density and effect of grazing on the standing crop measured in GTNP in spring ($F_{1,308} = 46.8, P < 0.001$). More vegetation was produced ($P < 0.001$) in areas of high elk densities than low elk densities, but more residual standing crop remained on grazed plots ($P = 0.027$) in low elk density than high density areas due to greater grazing offtake ($P < 0.001$) in areas of high than low elk density (Table 4). June temperature (inversely) and June precipitation (positively) best predicted annual vegetation production ($r^2 = 0.83, F_{2,4} = 10.1, P = 0.027$).

Timing of Fall Migrations

Initiation of migrations of TW–YNP elk was inversely related to cumulative snowfall through 10 November ($r^2 = 0.99, F_{1,1} = 353, P < 0.034$). Arrival dates of TW–YNP elk at the NER were earlier when mean monthly October temperatures were lower and snow depths achieved by 10 November at the south entrance of Yellowstone National Park were greater ($r^2 = 0.71, F_{2,7} = 8.4, P = 0.014$). However, no combination of October–November temperature, precipitation, and snow depth variables could explain >39% of the variation in when half of the elk population arrived

at the NER during 1982–2000. Presumably elk from GTNP, nearly half the wintering population, responded to different environmental cues than elk from the higher elevation and more distant summer ranges. For example, when the first radioed elk from GTNP arrived at the refuge each year (16 October–30 November) snow depths at Moran, Wyoming averaged 1.7 ± 1.4 cm.

Later migrations from GTNP followed summers of greater vegetation production. Measurements of standing crop at all sites and only at high elk density sites yielded equally predictive models of the mean migration date of GTNP elk to the NER ($r^2 = 0.89$ for each). Consequently, I used only measurements from high elk density sites in subsequent models of migration timing. For this 10-year period, I found that residual standing crop accounted for 82% of the variation in arrival of GTNP elk ($F_{1,8} = 36.1, P < 0.001$; Figure 4). Weather factors did not contribute significantly, but the number of elk on the NER the previous winter accounted for 39% of the residual variation in migration timing ($F_{2,7} = 4.9, P = 0.05$).

Arrival of 50% of the wintering herd at the NER was correlated with residual standing crop in areas of high elk densities ($r^2 = 0.75, F_{1,8} = 24.2, P = 0.001$). When elk numbers the previous winter at the NER were considered along with residual standing crop, 87% of the variance ($F_{2,7} = 23.0, P = 0.001$) in annual arrival of the wintering herd at the NER was explained.

Harvests and Winter Mortality

During 1990–2000, I monitored 376 migrations of GTNP radioed elk and 136 migrations of TW–YNP radioed elk. Among GTNP elk, 11.3% of those ar-

TABLE 4. Measurements of standing crop (g m^{-2}), residual standing crop, and percent offtake in areas of high and low elk densities in Grand Teton National Park, 1991–1997.

Measurement	Elk density	\bar{x}	SE	<i>t</i> statistic	DF	<i>P</i> value
Standing crop	High	15.7	1.8	5.9	166	<0.001
Standing crop	Low	8.9	0.9			
Residual standing crop	High	5.9	0.8	2.24	166	0.027
Residual standing crop	Low	7.3	0.7			
Offtake	High	62	3.0	12.0	12	<0.001
Offtake	Low	18	2.1			

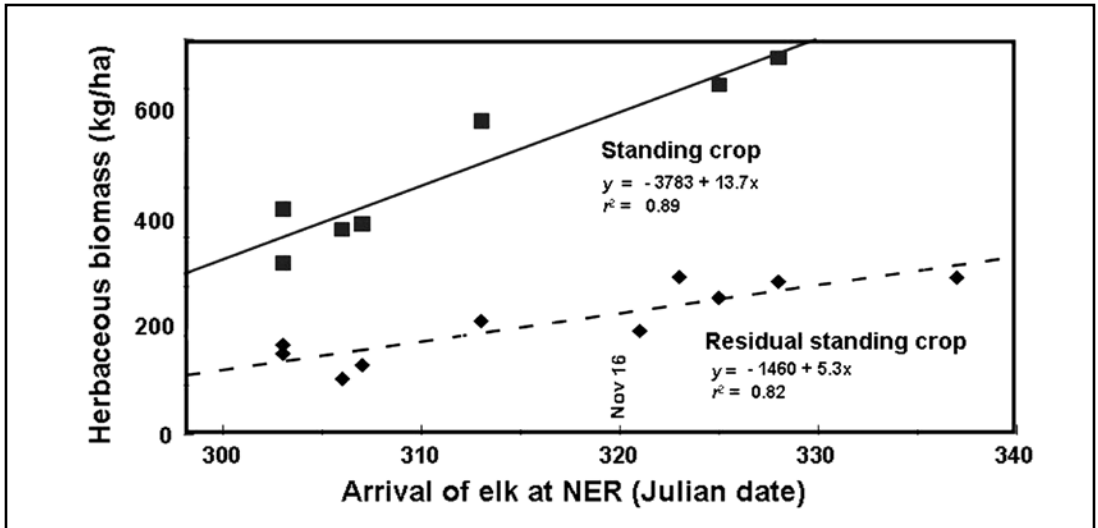


Figure 4. Relationship of elk migrations from Grand Teton National Park to the National Elk Refuge to measurements of annual standing crop and residual standing crop (vegetation remaining after summer-fall grazing) during 1991–2000.

iving after the median arrival date were harvested compared to 4.8% of early migrants ($\chi^2_1 = 4.4$, $P = 0.037$). Harvest rates were similar ($P = 0.25$) for TW–YNP and all GTNP elk. However, TW–YNP elk were harvested at a higher rate (10.3%) than early migrants to the NER from GTNP (4.8%, $\chi^2_1 = 4.2$, $P = 0.042$). More GTNP elk were harvested in Hunt Units 75, 76, 77, and 80 (25 of 27) than TW–YNP elk (7 of 14; Fisher’s exact test = 0.004). Mean harvest dates in those units were similar (15 November for GTNP elk, 21 November for TW–YNP elk, $t_{30} = 0.8$, $P = 0.42$). The other 7 TW–YNP elk were harvested in hunting units farther north (Figure 2). Animals that summered in GTNP and TW–YNP and were harvested on their summer ranges prior to fall migration were excluded from these analyses.

During 1990–2000, 17 additional radioed elk (14 calves and 3 adults, all from GTNP) that migrated to the NER died during winter unrelated to hunting. Although more late migrants (11 of 149) than early migrants (6 of 183) died, the difference was not significant ($\chi^2_1 = 2.6$, $P = 0.11$). When I combined harvested elk and winter mortalities, late migrants to NER suffered higher losses than early migrants ($\chi^2_1 = 6.9$, $P < 0.01$).

Discussion

My purpose was to understand spatial and temporal aspects of elk migrations and their relationships

to survival of elk. Timing of fall migrations of other Rocky Mountain elk populations has most often been correlated with snow accumulations on summer ranges (Morgantini and Hudson 1988, Irwin 2002). For example, Rudd et al. (1983) found that elk migrated from eastern YNP when snow accumulated to depths of 20 cm. Murie (1951), Anderson (1958), and Boyce (1991) cited snow accumulation on summer ranges as the proximal factor stimulating fall migrations to lower elevation winter ranges of the Jackson elk herd. However, I found a more complicated pattern than that.

In general, availability of suitable resources across summer/fall ranges was the ultimate factor controlling timing of Jackson elk migrations. Elk inhabiting the most distant, high-elevation summer ranges migrated as they became “food access limited.” Migrations of TW–YNP elk correlated with snow accumulations by 10 November ($\bar{x} = 21 \pm 4.4$ cm). In contrast, snow depths averaged <2 cm at Moran, Wyoming, when GTNP elk began migrations and averaged only 10.4 ± 2.8 cm on the mean dates of arrival at the NER. Thus, depletion of sufficient high-quality forage was the proximate factor cueing migration. GTNP elk were “food production limited.” The fact that GTNP elk migrated later when the standing crop was greater supported this hypothesis. Furthermore, TW–YNP elk that migrated west of the Snake River and staged in GTNP’s already

forage-depleted Central Valley arrived at the NER 2 weeks earlier than TW–YNP elk that migrated to the east, where elk densities were lower and forage less heavily grazed. A growing bison herd in Jackson Hole (122 in 1990 to 489 in 2000) possibly brought additional competition to limited forage resources in GTNP.

Vales and Peek (1996) also found that cues other than snow were important in initiating migrations of elk to Yellowstone National Park's northern winter range. In 1987 they found radioed elk arrived at winter range an average 16 days before snow began to accumulate on summer ranges. In 1988, following a severe drought, arrival averaged 29 days before snow accumulation. The primary effects of the 1988 summer drought were reduced grass production (Singer et al. 1989) and desiccation of grasses and forbs 2-3 weeks earlier than in 1987 (Vales and Peek 1996). Garrott et al. (1987) reported mule deer migrating to winter range before snowfall to access higher quality forage (irrigated, fertilized crops) that had not senesced. Nearly 1,500 ha of irrigated and subirrigated plant communities and an additional 8,500 ha of ungrazed upland habitats at the NER provide a similar attraction to elk.

Fryxell et al. (1988) noted that wildebeest sought green forage as grasses cured and became less suitable as food. They observed that "herbivore abundance is probably determined by food availability during periods of resource scarcity." Resources are typically scarce in winter and early spring in the northern Rockies but due to supplemental feeding at the NER (Smith 2001, Lubow and Smith 2004), fall may be the limiting season for GTNP elk.

Migrations and Harvests

Variations in fall migrations complicate achieving harvest objectives to limit elk populations (Irwin 2002). Elk that summered in GTNP required the least time, traveled the least distance, and arrived 11–29 days earlier at the NER each year than the other three herd segments. This provided a window in which primarily GTNP elk could be harvested in Hunting Units 75–77 and 80. However, early migrants from GTNP were harvested least. Consequently, efforts to reduce the GTNP herd segment as a proportion of the Jackson elk herd, by implementing longer hunting seasons and issuing additional antlerless permits during

the 1990s (Table 3; Wyoming Game and Fish Department 2001), fell disproportionately on late migrants.

Adaptation

McCullough (1985) and Boyce (1991) theorized that the evolutionary inertia behind migratory behavior in elk was likely the length of time that they could acquire high-quality succulent forage. It follows that elk migrate to high elevation summer ranges where nutritional quality of forage surpasses that at lower elevation ranges (Morgantini and Hudson 1988, Albon and Langvatn 1992) to improve lifetime reproductive success by optimizing food available to parents for lactation and for body and antler growth (McCullough 1985, Cook 2002). Yet as digestible energy, protein, and ad libitum intake rates of forage rapidly decline with plant maturation (Van Soest 1982), aggregated elk and grazers in general may rapidly exhaust supplies of high nutrient plant parts (Fryxell 1991). Eighty-seven percent of GTNP radioed elk summered west of the Snake River, including the Central Valley where elk densities were more than double densities elsewhere on summer ranges (Smith and Anderson 2001). Aggregation in GTNP's Central Valley may benefit elk by enhancing net primary production and maintaining vegetation at immature growth stages (Hobbs and Swift 1988, Fryxell 1991, Frank and McNaughton 1993), yet foster intraspecific competition as forage is depleted. Interference competition on staging areas may elevate nutritional stress, particularly given that staging coincides with the latter part of breeding season. Even when the total amount of forage available is not limiting, increases in animal density may drive deterioration in the nutritional status of individuals, suggesting an upper limit on the nutritional quality of diets obtainable by any given population (Hobbs and Swift 1985).

Ostensibly, migration of GTNP elk during October and early November from the security of their national park sanctuary into areas where they could see, hear and smell hunters appears maladaptive. I suggest that as vegetation senesced on the low elevation, high elk density summer ranges of GTNP, both quantity and quality of forage became inadequate. Migrations coincided with an average 62% offtake of herbaceous biomass. Consequently, by mid-fall elk "chanced" migrating through open hunting areas (Units 75-77, Figure 2) to access superior forage at the NER. Although

winter mortality on the NER is low (Boyce 1989, Lubow and Smith 2004), the surfeit of standing forage available to early migrants may foster what otherwise could be construed as reckless behavior. Such behavior should be selected over time if it enhances fitness—by increasing survival or lifetime reproductive success. I did not measure reproductive success of radioed animals, but Smith and Anderson (1996) reported similar calf:100 cow ratios across all summer ranges of the Jackson elk herd. I did find significant survival advantages of early migration by GTNP elk, despite wildlife managers' efforts to harvest more early migrants by advancing the opening dates of hunting in Units 75–77 (Table 3) from 25–31 October during the 1980s (Smith and Robbins 1994) to 5–20 October during the 1990s (Table 3).

Some mechanisms by which 95% of early migrants were able to escape harvest were evident. Elk commonly migrated en masse or at night to the NER (Smith and Robbins 1994). Elk were more difficult to harvest during the early stages of migration because of lower hunter participation, due to mild weather conditions and hunter perceptions that migrations were yet to begin. Where elk occupy national parks or similar sanctuaries during summer, fall migrations to distant winter ranges may be delayed to avoid entering hunted areas (Irwin 2002). I could not evaluate if delaying migration from GTNP or YNP was a successful strategy, because all radiocollared elk entered open hunting areas before hunting seasons closed during this study. Where elk move into sanctuary areas to avoid hunters (Brown 1985, Burcham et al. 1999) or migrate between adjacent summer and winter sanctuaries (Larkins 1997), managers are also challenged to design hunting seasons to limit elk numbers and subsequent overpopulation of ranges.

Elk may learn strategies to avoid hunters and at the same time optimize diets. I commonly documented punctuated migrations whereby groups of elk hop-scotched from one security area to another. These ranged from relatively inaccessible patches of habitat on national forest lands to jurisdictions closed to hunting. YNP elk that twice crossed the Snake River enroute to the NER undertook the most complex fall migrations moving from the security of YNP to GTNP and

then GTNP to the NER. Hasty passages through the Teton Wilderness could turn leisurely if animals escaped significant hunting pressure due to favorable weather or they lingered in patches of security cover, thus protracting migrations of some individuals to 9 weeks.

Management Implications

Closely monitoring a representative sample of a population can reveal fitness benefits of differing migratory strategies. Migratory behavior is largely learned by juvenile elk from their mothers (Murie 1951) and I found it was adaptable to changing environmental cues. Despite low heritability, migratory behavior is still subject to natural selection because genotypes that migrate at inopportune times will be eliminated (Boyce 1991). Complex temporal and spatial migratory patterns challenge wildlife managers' skillfulness to manage elk numbers across heterogeneous topographic and jurisdictional landscapes. Where harvests are designed without understanding migratory patterns, elk may be harvested disproportionately across their summer distribution.

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