Does Dispersal Help Regulate the Jackson Elk Herd?
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Does dispersal help regulate the Jackson elk herd?

Bruce L. Smith and Stanley H. Anderson

Abstract Elk (*Cervus elaphus*) that summer in Grand Teton National Park (GTNP) are part of the migratory Jackson elk herd and have been hunted in portions of GTNP since 1950 to control population size. Our purpose was to determine whether dispersal of juvenile elk from natal summer ranges (herd segments) contributed to limitation of population size and thereby reduces the need for hunting in GTNP. None of the 81 yearlings, 55 2-year-olds, and 25 3-year-olds captured and radiocollared as neonates during 1990–1992 dispersed out of the Jackson herd unit. However, 15% of radiocollared juvenile elk (yearlings and 2-year-olds) within the Jackson herd unit annually dispersed into or out of Grand Teton National Park during 1991–1994. Dispersal out of GTNP (12 of 94, 13%) to summer ranges of relatively lesser elk densities was similar (*P*=0.38) to dispersal into GTNP (8 of 43, 19%). Only 1 of 25 3-year-old radiocollared elk dispersed. Male-biased dispersal into GTNP was corroborated by greater yearling male:cow ratios of elk censused in GTNP than outside the park (*P*<0.001). Yearlings (14 of 81) and 2-year-olds (6 of 55) that dispersed to new herd segments experienced greater hunting mortality (32%, *P*=0.008) than those that did not disperse (10%), and harvest mortality was male-biased (*P*=0.003). These results suggest that dispersal out of the Jackson elk herd was not a population-regulating influence and dispersal out of Grand Teton National Park was not a limiting influence on growth of elk numbers in the park. We conclude that at current elk densities, which are artificially maintained by winter feeding, hunting remains a necessary control on elk numbers in Grand Teton National Park.

Key words age ratios, *Cervus elaphus*, dispersal, elk, fidelity, gene flow, hunting, mortality, population limitation, Wyoming

Dispersal of juveniles from natal ranges has been reported in many species of vertebrates, including elk (*Cervus elaphus*, Flook 1970, Craighead et al. 1972, Rickard et al. 1977, Houston 1982). In polygynous mammals forming matrilineal groups, such as elk, adult females are more likely to tolerate female than male offspring of previous years within their home ranges (Franklin and Leib 1979, Greenwood 1980, Clutton-Brock et al. 1982). Therefore, males are the sex most likely to disperse and juvenile dispersal played a minor role in regulating populations of elk (Craighead et al. 1972, Houston 1982, DeVergie 1989) and red deer (*C. e. elaphus*, Clutton-Brock et al. 1985).

Managers of elk and other game species benefit from understanding dispersal patterns in several ways: 1) population modeling requires knowing whether a population is closed, 2) designing and assessing sustainable harvests across a population's distribution requires integration of factors contributing to population growth and decline, and 3) protection of habitats requires identification of movement corridors that link seasonal ranges within and between populations.

Conservation biologists also have an interest in dispersal. Dispersing individuals that leave a population can promote outbreeding and influence growth trajectories of the populations losing and

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A 4-day-old calf of the Jackson elk herd equipped with an expandable radiocollar in June 1991.

receiving dispersers (Dobson 1979, Greenwood 1980, McCullough 1985). However, these same effects might be observed among discrete breeding groups, or demes, of a single population of animals that share one or more common ranges outside the breeding season. In that case, demes would be the metric of scale across which dispersal could be measured. State managers of ungulate herds routinely treat demes as herd segments and are challenged with designing hunting seasons that representatively harvest animals from several herd segments across a game herd's summer–fall distribution. In the migratory Jackson elk herd, Cole (1969) documented a dramatic increase in numbers of elk that summered in Grand Teton National Park (GTNP) following the park's expansion in 1950 and removal of cattle from large areas of GTNP during the 1950s. Three-quarters of the 7,000–9,000 elk that winter and are supplementally fed on the National Elk Refuge (NER) spend summer in GTNP or Yellowstone National Park, where they are largely protected from hunting

(Boyce 1989, Smith and Robbins 1994). Crowding and feeding this large number of elk on the NER is costly, damages woody habitats, and predisposes elk to diseases such as brucellosis (Boyce 1989; Smith 2001). The practice of hunting elk in portions of GTNP and on the NER, where they are maintained in excess of habitat carrying capacity by winter feeding, has been controversial (Thomas et al. 1984, Wood 1984, Boyce 1989). However, winter mortality of the Jackson elk herd is low, the Jackson herd has exceeded its population objective by 2,000–8,000 elk since 1987, and hunting on those federal lands has been important to control the herd's size (Boyce 1989, Smith and Robbins 1994).

For the past 35 years, a goal of the state and federal agencies that cooperatively manage the Jackson elk herd has been to reduce the number of elk that migrate through or summer in GTNP (Cole 1969, Smith and Robbins 1994). Although hunting regulations during the 1970s and 1980s were intended to achieve that goal (Boyce 1989, 1991; Smith and Robbins 1994), in 1991 densities of elk in GTNP were 2.5-fold that of densities in herd segments outside GTNP (Smith and Anderson 1996). Similar situations face United States and Canadian wildlife managers where elk and deer numbers have increased in national parks and residential sanctuaries and become difficult to control (Hess 1993, Kay and White 1995, Wagner et al. 1995, Jones 1997).

Boyce (1989) and Smith and Robbins (1994) detailed difficulties of controlling numbers of elk in GTNP and stressed the need to understand any regulatory role of juvenile mortality and dispersal. Should dispersal of juveniles out of GTNP prove to be an important mechanism of population regulation, it may reduce the necessity of the controversial elk hunts that occur in GTNP and the NER. Smith and Robbins (1994) showed that only 2% of radiocollared adult elk dispersed among herd segments, but they and Martinka (1969) reported that more yearlings summered in GTNP than expected statistically. Therefore, we investigated relationships of range fidelity and dispersal of juvenile elk to population dynamics and management of the Jackson herd. We evaluated dispersal at 2 spatial scales: the entire herd unit and herd segments, or demes, within the Jackson herd. Specifically, we examined whether 1) dispersal occurred out of the Jackson elk herd, 2) dispersal rates of juvenile (yearling and 2-year-old) elk among herd segments equaled dispersal of older animals, 3) dispersal out

of the GTNP herd segment (where elk densities are relatively high) equaled dispersal into GTNP, 4) dispersal was male-biased, and 5) dispersers and philopatric juveniles experienced similar mortality due to hunter harvest.

Study area

Cole (1969), Boyce (1989), and Smith and Robbins (1994) described the boundaries, topography, and vegetative communities of the range of the Jackson elk herd, which encompassed 5,195 km^2 in northwest Wyoming. Mean annual temperatures decreased and precipitation and snowfall increased from the NER northward to Yellowstone National Park (YNP, Smith and Robbins 1994). The weather station at Moran, Wyoming (2,069-m elevation), is 44 km north of Jackson and near the center of the calving areas where we captured calves. It receives 617 mm of precipitation annually. January and July monthly temperatures average -10.2° C and 15.7° C, respectively (National Oceanic and Atmospheric Administration 1992).

Elk of the Jackson herd migrate 10-90 km between winter and summer ranges that vary from 1,950 to >3,650 m in elevation. Summer–fall (breeding) distributions are subdivided into 4 geopolitically distinct ranges that we refer 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), the last 2 occurring on the Bridger-Teton National Forest (Figure 1).

Herd segment boundaries were based on distributions of radiocollared elk (Smith and Robbins 1994).

Adult elk are faithful to herd segments but commingle in winter on the NER and other winter ranges in the Jackson herd unit (Cole 1969, Boyce 1989, Smith and Robbins 1994). The proportion of elk wintering on the NER that also spent summer in GTNP increased from 29% during the 1960s (Cole 1969) to 48% during the early 1980s (Smith and Robbins 1994). During summer 1991, elk numbers within the Central Valley of GTNP averaged 5.9 elk/km^2 and densities of elk in similar habitats outside the park averaged 2.4 elk/km^2 based on aerial
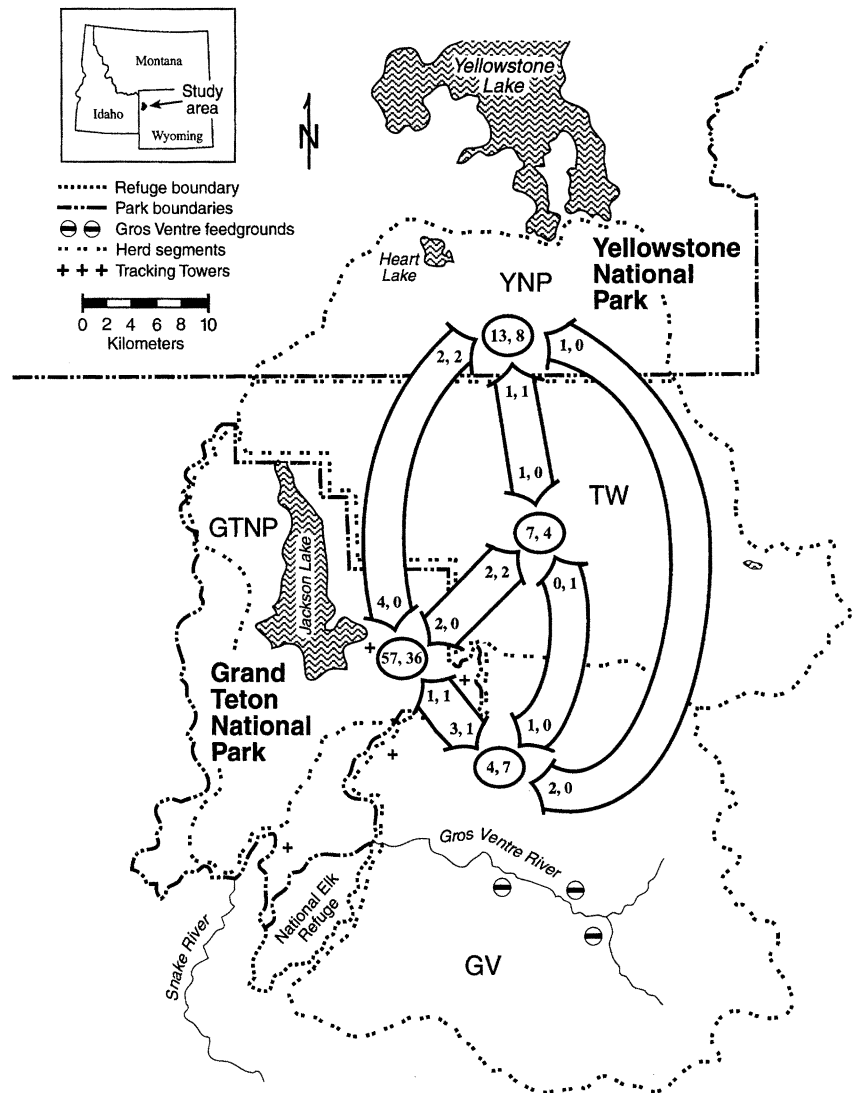

Figure 1. Number of radiocollared elk (calves, yearlings) that summered (circles) in the 4 herd segments of the Jackson elk herd (Grand Teton National Park [GTNP], Yellowstone National Park [YNP], Teton Wilderness [TW], and the Gros Ventre drainage [GV]), and dispersed (in arrow outlines as yearlings, 2-year-olds) among the herd segments during 1991–1994.

censuses, telemetry data, track counts, and harvests (Boyce 1989, Smith 1994).

Methods

Captures

During 27 May–8 June 1990, 26 May–9 June 1991, and 27 May–6 June 1992, we captured and radio-collared 164 newborn elk on traditional calving areas of all 4 herd segments of the Jackson elk herd (Smith and Anderson 1998). Smith and Anderson (1996) detailed the experimental design and sampling protocol. We followed animal welfare protocol as outlined by the University of Wyoming and the United States Fish and Wildlife Service at the time of the study.

Captured calves were manually restrained, blindfolded, hobbled, identified to sex and age, and weighed to the nearest 0.25 kg. Calves varied from <1 to 7 days old (mean=3.6±0.19) when captured (Smith et al. 1997), based on aging criteria of Johnson (1951). We fitted an expandable radiocollar (Telonics Inc., Mesa, Ariz.), designed to last for ≥26 months (3 summers), on each calf (Smith et al. 1998).

Monitoring radiocollared elk

We monitored radiocollared elk from May 1990 to December 1994 (Smith and Anderson 1996). From their capture through 15 July of each year, we located most calves once daily by triangulation from 4 fixed tracking towers (Figure 1). We located calves that migrated beyond the range of the towers from fixed-wing aircraft 3 times weekly. From 15 July to 1 December, we located elk 3 times weekly from ground stations or 2–3 times weekly from aircraft. During winter 1992–93, we chemically immobilized 44 surviving elk at NER feedgrounds and replaced expandable radiocollars with radiocollars designed for adult elk.

During the study, we monitored summer distributions of 120 captured calves that retained their collars and survived through September. We continued to monitor 81 as yearlings, 55 as 2-year-olds, and 25 as 3-year-olds.

Seasonal distributions, fidelity, and dispersal

"Calving areas" were locations where captured calves were born (Smith and Robbins 1994). We assigned each elk to a herd segment (GTNP, YNP, TW, and GV) based on the summer range it occu-

pied during July–October (Figure 1). Thirty percent of adult females calved in one summer range and after ≥1 week moved to another summer range.

We defined "fidelity" as return of an elk to the same herd segment, even if the geographic area occupied within the herd segment varied annually. "Dispersal" occurred at a coarse scale when an elk left the Jackson herd unit and did not return or on a finer scale when an elk occupied different herd segments within the Jackson herd unit in successive years. Dispersal is represented as a rate equaling the proportion of radiocollared elk that dispersed. Absolute numbers of elk dispersing from herd segments were unknown. Seasonal fidelity and dispersal of radiocollared elk that summered in GTNP were compared to all radiocollared elk that summered outside GTNP, because sample sizes from YNP, TW, and GV were small and comparisons had high Type II statistical error rates. We considered elk that remained on the NER during summer (<200 individuals) part of the GTNP herd segment (Cole 1969, Martinka 1969, Smith and Robbins 1994).

Herd classifications

During the first 2 weeks of August 1990 and 1991, we counted and classified elk inside and outside GTNP as calves, yearling males (antlers without brow tines), mature males (branch-antlered males with brow tines), or cows (yearling and older females) from a Bell Jet Ranger helicopter (Smith and Anderson 1996). We estimated yearling male:cow and mature male:cow ratios for each herd segment following Thompson (1992).

Statistical treatment

We used logistic regression to model dispersal rate as a function of age class (juvenile or adult), sex (male or female), and herd segment of origin (GTNP or other). We investigated 2-way interactions and main effects. We tested terms in the model for significance using an approximate drop-in-deviance F test (Venables and Ripley 1994). Terms deemed nonsignificant were dropped from the model.

We computed confidence intervals on estimated dispersal probabilities by bootstrapping (Manly 1997). We computed percentile bootstrap intervals by resampling, with replacement, observations from each age class and refitting the final logistic regression model. The 2.5% and 97.5% percentiles of 1,000 bootstrap estimates of dispersal rates

formed the lower and upper endpoints of our 95% confidence intervals.

We derived data used in the logistic regression analysis from all elk with known summer ranges in ≥2 consecutive years. If an animal changed herd segments between summers, we considered that animal a disperser. We regarded each animal that did not change herd segments between successive summers as a nondisperser. Thus, an elk that survived 3 years had 3 opportunities to disperse: calf to yearling, yearling to 2-year-old, and 2-year-old to 3-year-old. To obtain adequate sample sizes for analysis, we pooled elk from the 3 herd segments outside GTNP.

We also used logistic regression to determine whether differences existed in hunting mortality of radiocollared elk. The initial logistic regression equation included dispersal, age, and sex and all 2-way interactions of these variables. Again, terms deemed nonsignificant from the approximate drop-in-deviance F test we dropped from the model.

We used likelihood ratio chi-square to test goodness of fit of categorical data, including dispersal rates between yearlings and 2-year-olds and between herd segments. For data with less than 5 observations/cell, we used Fisher's exact test to test goodness of fit (Sokal and Rohlf 1981). We used Student's t-test to compare age ratios of elk in GTNP to elk that summered outside GTNP.

For game managers, emigration, dispersal, and variable survival can confound population estimates, harvest goals, and evaluation of management strategies. Maintaining sample sizes in studies of juvenile dispersal in hunted populations is difficult (Petersburg et al. 2000). We chose $P<0.10$ as significant for all statistical tests rather than a smaller P value, due to the biological and management importance of any such finding.

Results

Herd unit fidelity

From 1990 to 1994, we determined seasonal distributions of 92 calves captured in GTNP and 28 captured outside GTNP. Calves ($n=120$), yearlings ($n=81$), 2-year-olds ($n=55$), and 3-year-olds ($n=25$) occupied all 4 herd segments of the Jackson herd (Figure 1). Two female calves and one female yearling summered <5 km outside the Jackson herd unit in the upper Yellowstone drainage southeast of YNP. All 3 were within the Jackson herd boundaries the ensuing year. All but 2 elk, both yearlings,

remained in the Jackson herd unit during winter and both of those returned in summer.

Movement from calving areas to summer ranges

Thirty-seven of 120 calves captured during 1991–1992 moved to summer ranges geographically separate from their calving areas: 18 during June, 17 during July, and 1 each during August and September. Seventeen (11 males and 6 females) of 28 calves captured outside GTNP moved from their calving areas to geographically separate summer ranges (6 to YNP, 8 to TW, 3 to GV). Calving areas of the remaining 11 calves overlapped or were adjacent to their natal summer ranges, which were mostly in GTNP. Twenty (11 males and 9 females) of 92 calves captured in GTNP also traveled to summer ranges that were distinct from their calving areas (15 outside GTNP and 5 in GTNP).

Dispersal among herd segments

In our logistic regression analysis of dispersal rates, all interactions among sex, age, and herd segment and all main effects other than age were not significant. The probability of dispersal was greater ($P=0.073$) for juveniles (yearling and 2-year-old elk, 0.183, 95% CI = 0.113–0.252) than for adult elk (0.045, 95% CI=0.000–0.136).

Further examination showed that dispersal of yearlings into GTNP from natal ranges outside the park (7 of 24) exceeded dispersal of yearlings out of GTNP (7 of 57, $G_1=3.37$, $P=0.066$, Table 1, Figure 1).

Table 1. Age, sex and summer herd segment of origin of radiocollared elk that dispersed into Grand Teton National Park (GTNP) from other herd segments or out of GTNP to other herd segments during 1991–1994.

Herd segment of origin	Age	Sex	No. of elk that could have dispersed	No. of elk that dispersed
GTNP	Yearling	Male	25	2
Other	Yearling	Male	14	6
GTNP	2-year-old	Male	15	1
Other	2-year-old	Male	5	0
GTNP	3-year-old	Male	4	0
Other	3-year-old	Male	0	0
GTNP	Yearling	Female	32	5
Other	Yearling	Female	10	1
GTNP	2-year-old	Female	22	4
Other	2-year-old	Female	13	1
GTNP	3-year-old	Female	11	0
Other	3-year-old	Female	10	1

Table 2. Mature male:cow ratios (r) obtained during helicopter classifications of elk during the first 2 weeks of August 1990 and 1991. Ratios are compared between Grand Teton National Park (GTNP) and areas outside GTNP with Student's t tests.

Year	Area[a]	No. mature males	No. cows	r ± SE	Test result
1990	GTNP	114	359	0.318 ± 0.143	P = 0.32
1990	Outside GTNP	177	1,136	0.156 ± 0.034	
1991	GTNP	195	606	0.325 ± 0.130	P = 0.22
1991	Outside GTNP	278	1,964	0.142 ± 0.030	

[a] Southern Yellowstone National Park (YNP), the Teton Wilderness Area (TW), and the Gros Ventre drainage (GV) were surveyed outside Grand Teton National Park.

Dispersal of yearlings from each of the 3 herd segments outside GTNP averaged 54% during 1991–1993 (Figure 1). Annual variation in dispersal of yearlings from GTNP to herd segments outside GTNP ranged from 5 to 18%. Dispersal of 2-year-olds out of GTNP, pooled for 1992–1994, did not differ from dispersal of 2-year-olds into GTNP ($G_1 = 0.99, P = 0.32$, Figure 1).

Nine females from the 1990 cohort retained their radiocollars and survived to age 3. All 9 returned to the same summer ranges (6 in GTNP, 2 in YNP, and 1 in TW) they occupied as 2-year-olds, but 2 (one YNP and one TW elk) had occupied natal ranges in TW and GTNP, respectively.

From the 1991 cohort, 16 elk (4 males, 12 females) survived to age 3. Fifteen returned to the same summer ranges (8 in GTNP, 3 in YNP, 2 in TW, and 2 in GV) they occupied as 2-year-olds, but 3 (1 YNP, 1 TW, and 1 GV elk) had occupied natal ranges in GTNP. A 3-year-old female that summered in GTNP had summered in YNP the previous year, but as a calf and yearling summered in GTNP.

Herd composition and dispersal relative to sex

Mature male:cow ratios from herd classifications did not differ between GTNP and the other 3 herd segments (Table 2). However, yearling male:cow ratios were greater in GTNP than outside GTNP (Table 3). Correspondingly, yearling males dispersed at a significantly greater rate into GTNP (6 of 14) than out of GTNP (2 of 26, Fisher's exact test P = 0.014).

Mortality of dispersers

Of 20 juvenile elk that dispersed from their previous year's summer range, 9 (32%) were harvested by hunters compared to 11 of 109 (10%) nondispersing juveniles (Figure 1). There were no significant interactions among sex, herd segment, and age in the logistic regression model that examined mortality. Hunting mortality was related significantly to sex (P=0.003) and whether the animal had dispersed to a new herd segment (P=0.003, Table 4).

The disparity in mortality of dispersers was most evident in yearlings. Six of 7 yearlings (5 males, one female) that dispersed into GTNP were harvested that same fall, but only 1 male of 7 yearlings that dispersed from GTNP was harvested. This differential mortality of dispersers yielded similar ($G_1 = 0.47, P = 0.49$) net rates of yearling dispersal (proportion of elk that disperse from an area and survive that fall hunting season) into and from the GTNP herd segment.

Discussion and conclusions

Fidelity to Jackson herd unit

Boundaries of the Jackson herd unit were delineated by the Wyoming Game and Fish Department to encompass a distinct group of elk of which <10% would interchange with surrounding herds annually (Gasson 1987). Our findings confirm previous investigations that <5% of marked Jackson elk leave the herd unit boundaries (Straley 1968, Boyce 1989, Smith and Robbins 1994) and the few radioed

Table 3. Yearling male:cow ratios (r) obtained during helicopter classifications of elk during the first 2 weeks of August 1990 and 1991. Ratios are compared between Grand Teton National Park (GTNP) and areas outside GTNP with Student's t tests.

Year	Area[a]	No. male yearlings	No. cows	r ± SE	Test result
1990	GTNP	27	359	0.075 ± 0.003	P <0.001
1990	Outside GTNP	41	1,136	0.036 ± 0.002	
1991	GTNP	87	606	0.145 ± 0.006	P <0.001
1991	Outside GTNP	136	1,964	0.068 ± 0.009	

[a] Southern Yellowstone National Park, the Teton Wilderness area, and the Gros Ventre drainage were surveyed outside Grand Teton National Park.

Table 4. Harvest mortality rates of radiocollared, juvenile (yearling and 2-year-old), male and female elk relative to whether they dispersed or were faithful to their previous year's herd segment, 1991–1994.

Dispersed	Sex	Mortality rate	95% confidence interval
Yes	Male	0.587	0.390–0.759
No	Male	0.240	0.158–0.346
Yes	Female	0.232	0.114–0.414
No	Female	0.063	0.033–0.117

elk that left the herd unit did so only seasonally. The area of greatest commingling of adjacent elk herds on common summer range continues to be the Yellowstone River drainage in southeastern YNP and northeastern TW (Anderson 1958, Craighead et al. 1972, Rudd et al. 1983), where 3 of 120 elk in this study each spent 1 summer and 1 of those elk spent 1 winter. No radiocollared animals were harvested outside the Jackson herd unit (Smith 1994) and dispersal of elk out of the herd unit was apparently not a population-limiting factor.

Dispersal among herd segments

Dispersal occurred at the scale of herd segments—that is, among summer ranges within the Jackson herd unit. Contrary to our expectations, dispersal out of GTNP, where elk densities were greatest, did not exceed dispersal into GTNP. Three hypotheses explaining juvenile and subadult dispersal are: inbreeding avoidance, mate competition, and resource competition (Greenwood 1980, Dobson 1982). If density-dependent resource competition were to occur, we anticipated animals to disperse differentially out of GTNP. We consider dispersal of Jackson elk among herd segments as "presaturation" (density-independent) dispersal, as defined by Lidicker (1975), for the following reasons. First, rate of dispersal into GTNP was similar to dispersal to summer ranges out of GTNP, where elk densities were 0.4 times as great as in GTNP. Second, densities of Jackson elk (2.4–5.9/km²) were similar to summer densities in YNP during the late 1970s (≈2.1/km², Houston 1982) and the late 1980s (≈3.9/km², Singer et al. 1989) and 4–5 times less than densities of red deer on Rhum (Clutton-Brock et al. 1982). Juvenile dispersal did not contribute to population regulation of those herds. Third, Boyce (1989) reported that harvest rates of elk in GTNP approached maximum sustained yield,

limiting elk numbers in GTNP to about 75% of estimated K. Lastly, many density-dependent responses are nonlinear and would be fully expressed only at high population levels (Fowler 1978). Declining juvenile survival is among the first of measurable responses to increasing densities (Eberhardt 1977), but it was not documented in Jackson elk (Smith and Anderson 1998).

Age and sex related dispersal

Our results support the conclusion that most dispersal occurs before elk become 3 years old. Just 1 of 25 3-year-olds dispersed, which corroborates the 98% fidelity of elk ≥3 years old reported for the period 1978–1984 (Smith and Robbins 1994). High fidelity of adults to summer ranges has been reported in other migratory Rocky Mountain elk populations (Brazda 1953, Knight 1970, Craighead et al. 1972, Rudd et al. 1983, Brown 1985, Lyon et al. 1985). Strong range fidelity of adults likely contributes to high densities of elk in parks and other refuges where large predator densities are low and human exploitation is limited.

The male-biased dispersal of yearlings into GTNP explains Martinka's (1969) and our observations that more yearling males than expected summered in the GTNP herd segment. However, this pattern and the high fidelity of mature males to summer ranges (Smith and Robbins 1994) did not produce statistically greater mature male:cow ratios in GTNP than outside the park. This was largely a result of the variation in our estimates of mature male:cow ratios in GTNP (Table 3), which we believe was due to marked segregation of mature males from female–subadult groups across survey sampling units (S. L. Cain, Grand Teton National Park, and B. L. Smith, National Elk Refuge, unpublished data). Sexual segregation during summer occurs in red deer (Clutton-Brock et al. 1982) and elk (Flook 1970, Franklin and Leib 1979) and was implied for GTNP by Martinka (1969) and Boyce (1989).

The male-biased dispersal we observed was expected. Elk are polygynous, leading to greater competition for mates among males than females and to male-biased dispersal of juveniles (Geist 1982). However, yearling male:cow ratios were statistically greater and adult male:cow ratios were numerically greater in GTNP than outside the park. This apparently greater dispersal of males into GTNP, where elk densities were greater than outside GTNP, supports our inference that dispersal

among herd segments was not a consequence of resource competition.

We investigated alternative explanations for the greater yearling male:cow ratios in GTNP during this time period. Sex ratios of calves born in GTNP were not male biased and juvenile survival of calves born in GTNP was significantly greater in females than males (Smith et al. 1996). At 1 year of age, the male:female ratio of radiocollared elk that summered in GTNP favored females (84:100) and the sex ratio outside GTNP favored males (140:100, Smith and Anderson 1998). Thus, male-biased dispersal into GTNP is the most likely mechanism for greater year-ling male:cow ratios observed in GTNP (Table 3).

A radiocollared female elk on the National Elk Refuge partici-pating in the supplemental feeding program.

Sex-biased dispersal in our study may best be explained by the behavioral interactions of adult females and their previous year's offspring. Alt-mann (1956) reported that when pregnant cows of the Jackson herd dropped out of the spring migra-tion to calve in late May and early June, yearlings remained with them; the remaining elk continued migrating to more distant summer ranges in the TW and YNP. During calving, females become intolerant of yearlings, particularly males (Franklin and Leib 1979, Clutton-Brock et al. 1982, Geist 1982). Ander-son (1958) noted that some 2-year-olds, as well as yearlings, were segregated from calf–cow groups in early summer. These patterns would account for our observations and those of Martinka (1969) that numbers of yearling males decreased as distance increased from the NER winter range to the farthest summer ranges.

Yellowstone National Park, the summer range most distant from NER, experienced the greatest outward dispersal by juvenile males (Figure 1). Spring migration routes from NER to YNP pass through the central valley of GTNP (Smith 1994, Smith and Robbins 1994). Adult males arrive in YNP about 3 weeks in advance of adult females, which interrupt their migrations to calve south of YNP most years (Smith and Robbins 1994). We suggest that when parturient females resume migration in late June and July, they remain aggres-sive toward yearling males that are left behind in GTNP. Older males that yearlings may have joined (Altmann 1952, Franklin and Leib 1979) are likely to summer in GTNP because TW and YNP males would have migrated through GTNP earlier. Con-versely, yearling females rejoin adult females fol-lowing calving (Altmann 1956, Franklin and Leib 1979). Although migratory behavior and fidelity to seasonal ranges may be learned by elk calves from

their mothers (Murie 1951, Altmann 1956), male-biased dispersal of juveniles appears characteristic of polygynous mammals with matrilineal social sys-tems (Clutton-Brock and Harvey 1976, Greenwood 1980, Clutton-Brock et al. 1982). Although juvenile dispersal may function to reduce inbreeding, the cause of juvenile male dispersal may be social intol-erance and aggression by their mothers.

Harvest of dispersers

Dispersal has been correlated with increased exploitation rates of white-tailed deer (*Odocoileus virginianus*, McCullough 1979, Marchington and Hirth 1984) and moose (*Alces alces*, Houston 1968) populations and subsequent changes in animal den-sities. Twenty-one of 22 ≥1-year-old radioed elk mortalities in this study were taken by hunters (Smith and Anderson 1998). Hunting apparently altered the role that juvenile dispersal may play in differential growth of the herd segments. Dispersal was greater into than out of GTNP, but dispersing juveniles experienced greater harvest than nondis-persing juveniles did.

The high vulnerability of yearling, male dis-persers to GTNP was unlikely due to favorable hunting conditions in GTNP. Hunting regulations favor harvest of antlerless elk in GTNP and harvest rates in GTNP are similar to harvest rates elsewhere in the Jackson herd unit (Smith and Anderson 1998). Instead, we suspect the high vulnerability of yearling, male dispersers to GTNP and dispersers in general was attributable to their social grouping with other inexperienced juveniles (Murie 1951, Altmann 1952, Martinka 1969). Conversely, yearling females likely joined matrilineal social groups (Franklin and Leib 1979). Flook (1970) and Peters-burg et al. (2000) also reported high mortality

among yearling males that dispersed compared to those that did not disperse from natal summer ranges. By removing dispersing juveniles, as well as philopatric elk, hunting remains an important tool for managing the elk that summer in GTNP.
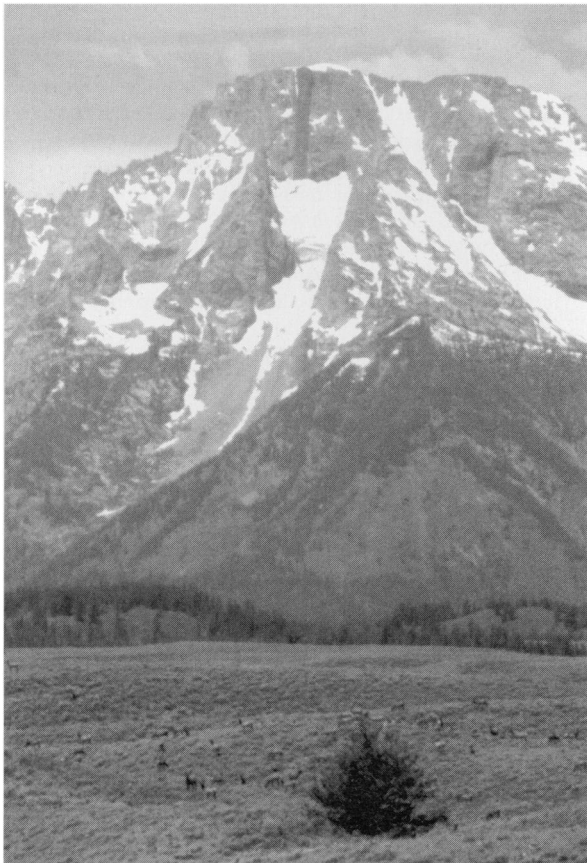
Management implications

Dispersal of elk out of the Jackson herd is minimal, enhancing the reliability of population modeling and design of harvest strategies, but restricting the role of dispersal in regulating herd size. Rates of dispersal of juvenile elk out of GTNP were similar to dispersal into GTNP from summer ranges of lesser elk densities. This finding, combined with a lack of density-dependent juvenile mortality or recruitment (Smith and Anderson 1998), suggests that culling of elk in GTNP and the NER remains necessary to control numbers of elk that spend summer in GTNP and to limit the total size of the Jackson herd. In other elk herds that occupy protected areas such as parks and residential areas, dis-

persal also may fail to limit population growth until elk densities approach or exceed K and produce resource limitations (Fowler 1987). Elk are long-lived, particularly where they are lightly hunted (Flook 1970). Dispersal is less likely to be of importance in old-aged populations because juveniles comprise a small proportion of the population and adult elk exhibit high fidelity to seasonal ranges. Furthermore, dispersal of juvenile elk is likely to be male-biased, with limited impact on population growth in this polygynous species.

Juvenile males suffered significantly greater mortality than females, in large part due to the vulnerability of dispersing males to hunting. In populations where dispersal rates are great, as reported in Colorado (Petersburg et al. 2000), differential harvest mortality of males may skew sex ratios in favor of females.

Dispersal of a population among relatively discrete summer ranges can have important conservation implications. Where migrations and dispersal have been disrupted or lost due to habitat fragmentation, access to food and other resources, including unrelated mates, may be impossible. Fidelity to summer–fall breeding ranges within a population's distribution and high mortality of dispersers may further limit the opportunity for gene flow. For large populations, such as the Jackson herd, this may be of negligible consequence. However, in low density, isolated populations, understanding movement and breeding patterns may advance conservation efforts to secure dispersal corridors and enhance genetic exchange among demes.

Elk on summer range in Grand Teton National Park, with Mount Moran in the background.

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