

Is the Migratory Behavior of Montane Elk Herds in Peril? The Case of Alberta's Ya Ha Tinda Elk Herd

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Abstract

There is growing concern that populations of migratory ungulates are declining globally. Causes of declines in migratory behavior can be direct (i.e., differential harvest of migrants) or indirect (i.e., habitat fragmentation or land-use changes). Elk (*Cervus elaphus*) are an important big game species in North America whose migratory behavior is changing in some montane ecosystems. We evaluated evidence and hypotheses for changes in migratory behavior and population decline in one of Canada's largest elk populations, the Ya Ha Tinda. We compared the ratio of migrant to resident elk (M:R) in the population and seasonal spatial distributions obtained from 22 winter and 13 summer helicopter surveys between 1972 and 2005. Timing of migration and the summer distribution for a sample of radiocollared elk also was compared for 1977–1980 (early period) and 2001–2004 (recent). The population M:R ratio decreased from 12.4 (SD = 3.22) in the early period to 3.0 (SD = 1.63). The decrease was greater than expected based on population change. Declines in M:R also mirrored behavior of radiocollared elk. More than 49% of radiocollared elk we monitored resided near the winter range year-round by 2001–2004, and migrants were spending less time on summer ranges. We found winter range enhancements, access to hay fed to wintering horses, recolonization by gray wolves (*Canis lupus*), and management relocations of elk were most consistent with observed elk population growth (adjusted for harvest and removals) and the change in migratory behavior. However, we could not isolate the effects of specific factors in time-series population modeling. We believe directly relating migrant and resident demography to habitat and mortality factors will be required to understand the mechanisms affecting migratory behavior in this and other montane elk herds. (WILDLIFE SOCIETY BULLETIN 34(5):1280–1294; 2006)

Key words

Alberta, Canada, *Canis lupus*, *Cervus elaphus*, elk, habitat enhancement, habituation, migrant:resident ratio, migration, prescribed fire, winter range, wolf.

Migratory ungulates, such as wildebeest (*Connochaetes taurinus*) in the Serengeti-Mara ecosystem, elk (*Cervus elaphus*) in the greater Yellowstone ecosystem, and barren-ground caribou (*Rangifer tarandus*) in the Arctic occupy a “keystone” ecosystem role, often defining and shaping ecosystems by their movements and effects on terrestrial processes such as herbivory and predator–prey dynamics (Houston 1982, Fancy et al. 1989, Sinclair 2003, Johnson et al. 2005). Because of their critical ecosystem role, concern for worldwide changes in migratory behavior of ungulates is mounting (Schaller 1988, Berger 2004, Johnson et al. 2005). The reasons for these changes usually are complex and variable but can be a result of direct (e.g., overharvest) or indirect causes (e.g., habitat fragmentation).

In Africa encroaching cultivation and poaching threaten the Serengeti wildebeest migration (Thirgood et al. 2004),

while in Asia, market hunting has been directly responsible for population declines of migratory Mongolian gazelles (*Procapra gutturosa*), Saiga antelope (*Saiga tatarica*), and Tibetan antelope (*Pantholops hodgsonii*; Schaller 1988, Lhagvasuren and Milner-Gulland 1997, Arylov et al. 2004). In North America many migratory populations underwent similar declines historically because of direct overharvest; for example, elk (Toweill and Thomas 2002). Recently, however, many populations have also faced indirect causes of migratory decline that has changed the relative benefits of migrating, favoring growth of nonmigratory segments of populations. For example, recent North American migratory declines have been attributed to differential hunting pressure on migratory segments of elk herds (Boyce 1989, Smith and Robbins 1994), habitat fragmentation associated with oil and gas development for pronghorn (*Antilocapra americana*; Berger 2004), diamond mine exploration for barren-ground caribou (Johnson et al. 2005), hydroelectric developments for woodland caribou (*R. tarandus*; Mahoney and Schaefer 2002), and also by creation of agricultural crops that, when combined with hunting

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sanctuaries, attract elk year-round (Burcham et al. 1999). Recovering wolf populations (*Canis lupus*) also may influence ungulate migrations. In western Canada a 10-year decline in the ratio of migrant to resident elk in the Bow Valley (BV) elk herd of Banff National Park (BNP) was correlated with human activity that created a predation refuge from wolves recolonizing these areas (Woods 1991, McKenzie 2001, Hebblewhite et al. 2005). Across much of western North America, ungulate populations are faced with similar indirect and complex land-use changes that may threaten the long-term viability of migratory populations (Smith and Robbins 1994, Berger 2004, Johnson et al. 2005).

We examined population and migratory dynamics of the Ya Ha Tinda (YHT) elk population in BNP from 1972 to 2005 to determine if migration behavior had changed, evaluate the consequences of migratory change to population dynamics, and evaluate possible management and ecological factors affecting migration. In the 1970s, almost the entire YHT population migrated 25–50 km west to summer inside BNP (Morgantini and Hudson 1988). Since the late 1990s, concern has been mounting that the decline in migratory behavior of the YHT elk herd is mirroring that observed in the Bow Valley of BNP a decade earlier. We focused on the YHT elk herd because it is the largest elk herd in BNP and one of the largest migratory herds in Canada (Gunson 1997). The herd winters outside of BNP on the low-elevation grasslands of the YHT winter range. Although this area was removed from BNP in 1931, Parks Canada retained ownership of a 44-km² ranch for training and wintering 100–200 horses on the winter range. Despite federal ownership by Parks Canada, however, management of natural resources is under Alberta provincial jurisdiction on the YHT. This transboundary setting leads to differences in federal and provincial management objectives (Morgantini 1995, sensu Clark et al. 2000), for example, controversy over horse versus elk overgrazing (McGillis 1977, AGRA Earth and Environmental Ltd. 1998), differences in predator management (protected inside BNP), and the restoration of fire as a natural disturbance (White et al. 1998). We took advantage of this transboundary study design to make a priori predictions about how 8 management and ecological factors would influence elk migration, and we tested whether predictions were consistent with observed changes in the migrant-to-resident ratio in the population (M:R), seasonal spatial distribution, and elk population dynamics using a broad hypothetico-deductive approach.

Study Area

The study area included the front and main ranges of the Canadian Rocky Mountains in BNP (51°30'N, 115°30'W) and adjacent provincial lands, and was defined by movements of the YHT elk herd over a 6,000-km² area (Fig. 1). Elevations ranged from 1,600 m in valley bottoms to 3,500 m. The study area lay along the eastern slopes of the Rocky Mountains, with long, cold winters and short growing

seasons during June–August. Vegetation was classified into 3 ecoregions: montane, subalpine, and alpine. The montane ecoregion offered prime elk winter habitat and was dominated by lodgepole pine (*Pinus contorta*) interspersed with Engelmann spruce (*Picea engelmannii*)–willow (*Salix* spp.) areas, aspen (*Populus tremuloides*)–parkland, and grasslands. Subalpine and alpine ecoregions were composed of Engelmann spruce–subalpine fir (*Abies lasiocarpa*)–lodgepole pine forest interspersed with willow–shrub riparian communities, subalpine grasslands, and avalanche terrain grading to open shrub–forb meadows in the alpine ecoregion. Holland and Coen (1983) provide a detailed description of study area vegetation. Ya Ha Tinda means “mountain prairie” in the Stoney-Sioux language, aptly describing the azonal, high-elevation, 20-km² montane rough fescue (*Festuca campestris*) grasslands along the north side of the Red Deer River (Fig. 1). The YHT represents one of the most pristine and largest rough fescue montane grasslands left in Alberta (Willoughby 2001). The area was mixed with aspen forests, open conifer stands, willow–bog birch (*Betula glandulosa*) shrublands and was surrounded by pine grading to spruce forests at higher elevations. Grassland soils consisted of azonal prairie types, including rich Orthic Black and Eluviated Black Chernozem (McGillis 1977, AGRA Earth and Environmental Ltd. 1998).

Elk were the most abundant ungulate in the study area during the past 3 decades, ranging from 1,500 to 2,500 animals (Holroyd and Van Tighem 1983), and constituted 70% of wolf diet (Hebblewhite et al. 2004). The YHT elk herd was partially migratory, with polymorphism for migrant and resident behavior. Migrant elk departed the winter range in May or June for summer ranges, returning to winter ranges from late September–December (Morgantini 1988). Despite this movement into BNP in summer, elk from the YHT herd have shown little interchange with other park elk herds (Morgantini and Hudson 1988, Woods 1991). The YHT elk herd wintered outside BNP in the province of Alberta in 1 main and 2 secondary winter ranges (Fig. 1). The primary winter range for approximately 90% of the elk herd (Hebblewhite 2006) was the YHT (Wildlife Management Unit [WMU] 418; Fig. 1). The 2 secondary ranges included the Panther–Dormer river corners (WMU 416) and Harrison–Lost Guide creek flats (WMU 420).

Although elk dominated, white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), mule deer (*O. hemionus*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and a remnant herd of 5–8 mountain caribou (*R. tarandus*) also occurred. Alternate prey species population trends are less well-known, but bighorn sheep have been relatively stable while deer species, moose, goat, and caribou numbers appear to have declined in the study area since the mid-1980s (T. Hurd, Parks Canada, Banff National Park, unpublished data). See Hebblewhite et al. (2004) for more information on wolf predation in this multi-prey system. Other carnivores included grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*).

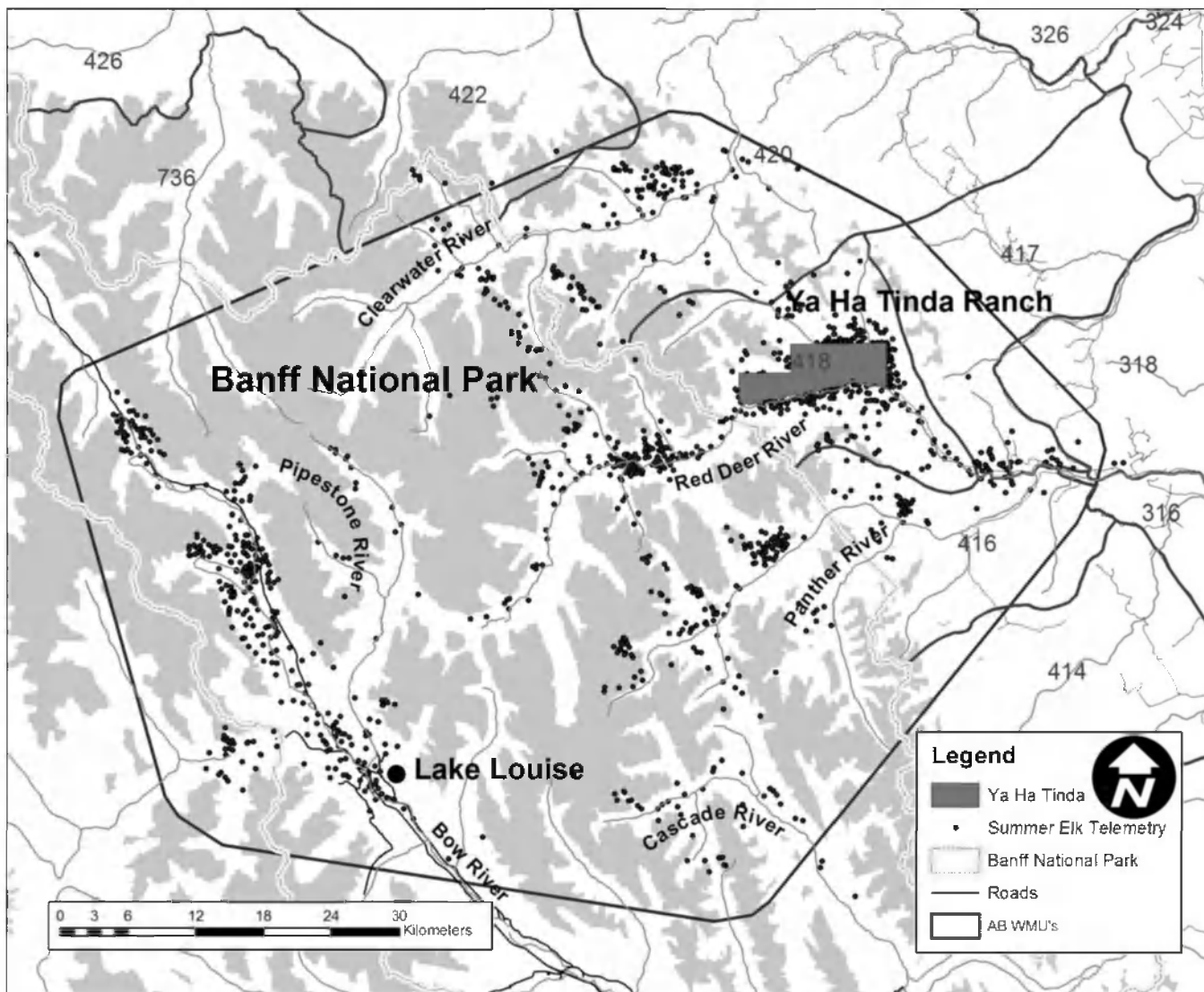


Figure 1. Location of the Ya Ha Tinda elk population study area on the eastern slopes of Banff National Park, Alberta, Canada, showing Ya Ha Tinda Ranch, major rivers, Alberta Wildlife Management Units (WMUs), and distribution of radiocollared elk from 2001 to 2004 during summer. Areas above 2,300 m are shaded gray.

Methods

We tested for evidence of migratory changes and evaluated hypotheses underlying migratory patterns in the YHT population. We synthesized data collected over the 1972–2005 period to test for migratory changes from 3 major data sources: one early telemetry study from 1977 to 1980 (Morgantini and Hudson 1988), federal and provincial aerial survey and visual neck-banding data from 1970 to 2004, and one telemetry study during 2002–2004. Further, we identified 8 hypotheses as potential causes for migratory declines that fell into 3 broad categories: elk population management, habitat management, and wolf predation-related (Table 1). Because migratory elk historically remained in BNP until after the regular autumn elk harvest outside BNP ended (Morgantini 1988), we predicted that autumn harvests would reduce residents more than migrants, thus increasing the M:R ratio (Table 1: H1 [Hypothesis 1]) and, given sufficiently high harvests, reduce

elk population size (N_t) and population growth rate (r_t). Second, more than 1,000 elk were relocated from YHT in the 1990s. If no bias occurred during capture, we would expect no change in M:R following relocation. Thus, changes in M:R following relocation suggest relocation-influenced migration (Table 1: H2).

Prescribed fires occurred over the past 2 decades on the summer range of migratory elk in BNP (White et al. 2003). The positive effects of fire on elk (Boyce and Merrill 1991, Taper and Gogan 2002) would favor migrants, increasing M:R (Table 1: H3). In contrast, we expected winter range habitat enhancements would benefit resident elk more than migratory elk, thus decreasing the M:R ratio, because residents inhabited the enhanced winter range year-round (Table 1: H4). In either case, habitat enhancements also would be expected to increase N_t and r_t . If competition between elk and horses was limiting access to forage, a reduction in number of horses would be expected to increase

Table 1. Hypotheses (H1–H8) for effects of different classes of management actions and their predicted effects on migratory behavior and population size of the Ya Ha Tinda (YHT) elk herd, Alberta, Canada, 1970–2005. Management actions are predicted to increase (+) or decrease (–) the proportion of migrants and overall population size (N). Observed trends in the ratio of migrant to resident elk (M:R) and population size over the 30-year period are presented for comparison. Predictions in boldface matched observations.

Management action	Hypothesis	Predicted effect on		Mechanism	Observed change		Consistent with	
		M:R	N^a		M:R	N^a	M:R	N^a
H1: Elk harvest	Differential harvest of resident elk should cause M:R to increase.	+	–	Elk harvest disproportionately reduces residents because most migrants do not return to the YHT for the whole hunting season.	–	+	No	No
H2: Elk relocations	Removal of 1,044 elk from YHT caused migrants to decline.	–?	– ^b	Capture bias for migrant elk would reduce migrants and/or disrupt learned migratory behavior.	–	– ^b	Yes	Yes^b
H3: Prescribed fire	Burning on summer ranges should increase migrant elk.	+	+	Burning increased forage in predominantly conifer burns available to migrant elk (Sachro et al. 2005).	–	+	No	Yes
H4: Winter range enhancements	Winter range enhancements increase resident elk numbers.	–	+	Resident elk remain on winter range all year, benefiting from enhanced forage during summer as a result of habitat enhancements (Morgantini 1995).	–	+	Yes	Yes
H5: Winter horse numbers	Declining horse numbers released elk from range competition (McInenely 2003).	–	+	Fewer horses should increase elk and decrease M:R ratio because resident elk increase due to carry-over effects of winter horse grazing in summer.	–	n/a ^c	Yes	No ^c
H6: Hay feeding	Prolonged access to artificial food source contributed to migratory decline.	–	+	Hay feeding increased habituation of residents and reduced migration (Burcham et al. 1999).	–	+	Yes	Yes
H7: Wolf predation	Spatial separation through migration reduced relative predation risk for migrants.	+	–	Migrant elk should have lower predation risk (Bergerud et al. 1984), but recolonizing wolves would still be predicted to reduce elk population size (Hebblewhite 2005).	–	+	No	No
H8: Provincial wolf harvest	Differential harvest of wolves in province surrounding YHT reduced predation on resident elk.	–	–	Wolf protection in Banff National Park would reverse the relative benefits of migration under the spatial separation hypothesis; overall, elk N still decline (Hebblewhite 2005).	–	+	Yes	No

^a Note predicted effects of hypotheses on N_t and r_t are the same.

^b Overall population increased but declined following relocations. This prediction was only compared to the postrelocation time period.

^c Horses only started declining (Table 2) following elk relocations, and during this period elk numbers were stable (Fig. 2) as a result of release from competition after relocation.

elk N_t and r_t . Residents may be expected to benefit more because residents remain on the winter range year-round and would benefit most from carry-over effects of reduced winter horse grazing on summer forage availability (Table 1: H5; McInenly 2003). Open access to hay fed to horses during late winter may be associated with elk habituation to humans, which may reduce M:R over time (e.g., Burcham et al. 1999) but with uncertain effects on elk population dynamics (Table 1: H6).

In addition, wolves were just recolonizing the study area during the late 1970s and were considered established by the early 1980s (Morgantini 1988). Migration is broadly hypothesized to reduce predation risk for migrant ungulates (Bergerud et al. 1984, Fryxell et al. 1988). If true, migration would be expected to increase the M:R ratio (Table 1: H7). However, as an extension to this hypothesis, wolf protection in BNP led to higher wolf survival between 1987 and 2000 than adjacent provincial areas where wolves were harvested (Callaghan 2002). If harvest was sufficiently high, survival differences could translate to higher relative wolf densities inside BNP, which could reduce the M:R ratio (Table 1: H8). In an additive fashion to any direct gradient, high human activity on the YHT during summer may cause wolf avoidance (Theuerkauf et al. 2003), potentially benefiting resident demography and decreasing the M:R ratio similar to the BV elk herd (Hebblewhite et al. 2005). Regardless, as an important limiting factor, predation by recolonizing wolves should reduce overall elk N_t and r_t (Hebblewhite 2005).

We used a broad hypothetico-deductive framework to examine predictions of these 8 hypotheses in comparison to observed population response and change in M:R ratio (Table 1). If the predicted effect of a management hypothesis was consistent with observed changes in M:R population trend and helped explain elk population growth rate, we considered this strong evidence that the hypothesis influenced migratory and population dynamics. If a management hypothesis was related to M:R but not N_t or r_t , we considered this weaker evidence of an overall migratory effect. Finally, if a management hypothesis was consistent with elk r_t or N_t but not M:R, we concluded the management hypothesis affected migrants and residents equally.

Elk Capture and Monitoring

We captured elk during 2 separate studies approximately 20 years apart, using 1 corral trap during the 1971–1980 study and 2 corral traps during the 2002–2004 study. We deployed visual neck collars on 11 adult females in 1971–1973 and 11 radiocollars (Telonics Inc., Mesa, Arizona) in 1977–1980 (7 adult F, 1 M and 2 F yearlings, 1 M calf), such that during 1977–1980 there were 22 marked elk in the population. In 2002–2004 we marked 59 elk (50 adult F, 9 F yearlings) with very high frequency radiocollars (LOTEK Inc., Aurora, Ontario, Canada) and 20 elk (18 adult F, 2 F yearlings) with Global Positioning System (GPS) 2200 or 3300 collars (LOTEK Inc.). We captured all elk on the main YHT winter range between January and March of each year

when migrant and residents mix in large groups. Association matrices confirmed thorough mixing of migrants and residents during winter (Hebblewhite 2006). Capture locations between studies were similar; one corral trap in both studies was located <1 km apart, and during 2002–2004 we used a second trap 3 km east of the first trap to minimize potential capture bias. During both periods we relocated radiocollared elk biweekly, either from the ground or aerially from fixed- or rotary-wing aircraft. During the early 1977–1980 period, we resighted 9 neck-banded elk an average of 3.3 times/summer but 2 were never sighted again, suggesting potential sightability bias (see Morgantini 1988). Because of different sampling intensities (GPS collars vs. neck-bands), we used collared animals to assess M:R ratio and simple watershed distribution patterns between studies. Research was conducted according to University of Alberta Animal Care Protocol 353112, Parks Canada EIA permit BNP-00047531, and Alberta research and collection permits GP4618 and CN087.

Changes in Migration Behavior

We evaluated the M:R ratio, seasonal (spring and autumn) migration dates, and the distribution of radiocollared elk. We calculated population-level M:R ratio using the maximum number of elk observed from air or ground during summer on the YHT winter range as a proportion of the following winter's aerial count. We compared population-level M:R between early (1977–1987) and late (1988–2004) periods using an unbalanced *t*-test. As a second measure, we compared M:R ratio of both radiocollared and neck-banded elk between the early and late intensive study periods of 1977–1980 and 2002–2004. Despite winter herd mixing and our capture precautions, we tested for bias by comparing the M:R ratio of captured elk to the population M:R ratio during each year using chi-square tests.

We defined migration as seasonal movement between allopatric home ranges and estimated migration date as the midpoint between subsequent telemetry locations on alternate migratory ranges (Craighead et al. 1972). We compared spring and autumn migration date by calculating the probability of early and late migration dates differing under the Z-approximation to the normal distribution (Sokal and Rohlf 1995). We had no information on duration of migration for the early period. Thus, we assumed duration was similar to late period GPS-collar estimates of 5 days (M. Hebblewhite, University of Montana, unpublished report). Whether the proportion of collared elk (both radio and visual neck-bands) on summer ranges identified by Morgantini (1988) changed between early and late periods was tested using a chi-square test (Sokal and Rohlf 1995).

Spatial Distribution

Parks Canada or the Alberta Fish and Wildlife Division conducted aerial surveys in rotary-wing aircraft (Bell 206B JetRanger, Fort Worth, Texas) every winter since 1972 except 1974, 1975, 1984, and 1989 (Table 2), and approximately every third summer since 1977 (1977, 1978,

Table 2. Time series of elk data and potential factors influencing temporal population dynamics of the Ya Ha Tinda (YHT) elk herd (Wildlife Management Unit [WMU] 418), 1970–2005, Alberta, Canada. Elk data include winter elk count (N_t) and maximum summer count of residents (N_{R-t}) on YHT. Population factors include the total Jun–Aug precipitation, Banff National Park (BNP) wolf abundance index, number of elk translocated, total number of elk harvested, winter horse numbers, cumulative area (km^2) burned in the provincial and BNP portions of the study area, and cumulative area (ha) of winter range habitat enhancement projects.

Year ^a	WMU 418 winter elk count N_t^a	Maximum summer resident count N_{R-t}^b	Jun–Aug precip. (mm) ^c	No. of BNP wolves ^d	No. of elk relocated	Total elk harvest ^e	No. of horses ^f	Cumulative burn area (km^2)	Cumulative winter range enhancements (km^2)
1973	807		277.2	9		133		0.0	0.0
1974	356		78.4	5		124		0.0	0.0
1975	351		78.8	11		33		0.0	0.0
1976	334		194.2	4		53		0.0	0.0
1977	358	34	125.3	4		56	186	0.0	0.0
1978	278	25	97.3	5		92		0.0	0.0
1979	422	25	203.4	5		135		0.0	0.0
1980	378		88	5		74		0.0	0.0
1981			174.3	10		170		0.0	0.0
1982	217		354.4	7		130		0.0	0.3
1983	200		182.1	16		186		0.0	0.5
1984	1058	75	221.1	23		160		0.0	0.8
1985	620	50	127.2	21		126		0.0	1.0
1986			77.9	20		76		4.2	1.3
1987	758	75	298.5	18		124		4.2	3.0
1988	918		209.3	25		150		4.2	6.9
1989	1075		180.4	29		170	180	6.5	7.7
1990	1052		140.6	30		181	183	21.6	8.0
1991	1285		245.6	35		68	196	21.6	8.3
1992			179.5	24		65	171	21.6	8.5
1993	2099		262.6	30		65	189	21.6	8.8
1994	1074		257.1	35	229 ^g	67	190	43.0	9.0
1995	1534		370.6	24	132	67	152	43.0	9.3
1996	1642		99.6	25	324	78		43.0	9.5
1997	952		163.6	35	139	67	146	43.0	9.8
1998	901		313.4	31	135	121		43.0	10.0
1999	976		129.1	25	85	87	153	45.7	10.3
2000	843	200	178.6	25		91	155	63.8	10.5
2001	931	150	187.3	26		65	144	63.8	10.8
2002	991	324	73.9	36		98	147	130.1	11.0
2003	916	259	83.2	32		107	127	130.1	11.3
2004	848	267		29		118	95	130.1	11.5
Mean	829.1	121.7	188.6	19.1	29.8	105.5	160.9	25.3 ^h	4.8 ^h
SD	412.01	106.77	84.89	11.49	74.45	40.18	27.8	38.3	4.7

^a Year 2004 refers to biological year 2003–2004 from 1 Jun 2004 to 31 May 2005.

^b Maximum number of resident elk counted on winter range WMU 418 during summer (1 Jun–31 Aug).

^c Total precipitation (mm) for Jun, Jul, and Aug reported at Blue Hill Tower Environment Canada weather station.

^d Wolf population index derived in Hebblewhite (2006).

^e Elk harvest includes all age classes, and elk killed by guides, resident, nonresident, and native hunters.

^f Number of horses wintered at YHT includes brood mares and horses being trained.

^g Only elk that did not return to YHT following relocation (Alberta Fish and Wildlife Division, unpublished data).

^h Mean annual area burned or enhanced.

1979, 1980, 1982, 1983, 1984, 1985, 1987, 1991, 1998, 2003, 2004). We conducted surveys 100–200 m above ground level at 50–70 km/hour. We conducted summer surveys in July during the morning (0600–1200 hours) on clear sunny days when elk were on high-elevation summer range and sightability was highest (Anderson et al. 1998). During summer surveys, we surveyed all alpine and subalpine summer elk ranges and key winter ranges identified by Morgantini and Hudson (1988). Telemetry data from both early and late periods confirmed no major summer ranges were missed during surveys (Morgantini and Hudson 1988, M. Hebblewhite and L. Morgantini, University of Montana, unpublished report). We flew

winter aerial surveys 1–2 days after heavy snowfalls during the morning (0800–1200 hours) on sunny or flat-light days during January or February to maximize sightability of elk (Allen 2005). We photographed large herds (>50) for counting. Continuous participation since 1972 by one author during winter surveys and by another author during summer surveys during both periods (early and recent) ensured data consistency. Only winter population counts, not spatial data, were available for aerial surveys from 1972 to 1977. After 1977 we recorded herd size, general herd composition (male, female, mixed), activity, and location and later transcribed these data to Universal Transverse Mercator coordinates. We considered locations accurate

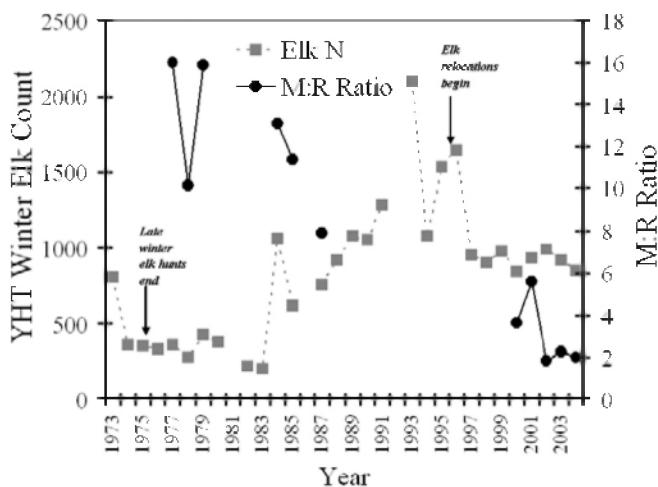


Figure 2. Winter aerial survey counts of elk from 1973 to 2004 in Wildlife Management Unit 418, Alberta, Canada (■), and migrant-to-resident ratio (M:R) of elk (●). End of the late-season elk hunt and elk relocations are shown.

only to 500 m because of mapping differences over time. Agency biologists occasionally conducted surveys in another agency's jurisdiction. When surveys overlapped in the same year, we used only agency area-specific data. Because aerial survey area sometimes varied, we used the 90% kernel of aerial elk sightings to define core seasonal survey areas. For each season we compared the spatial distribution of elk between time periods using multiple-range permutation procedures (MRPP; Berry and Mielke 1983) in program BLOSSOM (Cade and Richards 2001). The MRPP compares intra-group Euclidean distances with distances calculated at random (Berry and Mielke 1983) and tests the hypothesis that the spatial distribution of locations does not differ between ≥ 2 sampling occasions.

Factors Influencing Migration

We obtained number of elk harvested during regular hunting seasons by resident and nonresident (outfitter) hunters from 1972 to 2004 from WMU 418 (Fig. 1), from registered hunter phone surveys (Alberta Fish and Wildlife, unpublished reports) from 1986 to 2004, and from registered harvests prior to 1986 (Table 2). Hunting by First Nations is unreported and unregulated in Canada, but we obtained field estimates of First Nations harvest during years with field research and by Parks Canada ranch staff (Parks Canada, Ya Ha Tinda Ranch, unpublished data). Late-season hunts occurred after aerial surveys in January–February of 1969–1975, and elk harvest during these hunts were recorded at game-check stops and by registration (Alberta Fish and Wildlife, unpublished annual harvest reports).

Concern for overgrazing grew in the early 1990s as the YHT elk herd exceeded 2,200 elk (Fig. 2), and Alberta Fish and Wildlife Division (ABFW) relocated elk instead of allowing controversial late-season hunts to mitigate overgrazing concerns (Gunson 1997). From 1994 to 1999, 1,273 elk (Table 2) were relocated from YHT to locations 20–100

km away. During the first year approximately 50% (223) returned to YHT. By the second year elk were moved far enough away that return rate was $<10\%$ (Alberta Fish and Wildlife, unpublished data). Thus, we adjusted number of elk translocated by 50% during the first year (Table 2).

Within BNP Parks Canada burned an average of 5.04 km² (0–25.4 km²; Table 2) per year of predominantly coniferous pine and spruce forest (81% conifer; White et al. 2003, Sachro et al. 2005) for a total of >88.0 km² burned since 1986. In the provincial portion of the study area, one prescribed burn of 7.01 km² was conducted in 1994 in WMU 420, and one human-caused fire burned >60.0 km² during autumn 2001 in WMU 416. Fires only occurred in areas inhabited by migrant elk during summer. Because of delayed effects of fire on elk forage (Sachro et al. 2005), we used an index of cumulative area burned (White et al. 2005) to investigate fire's effects on elk (Table 2).

Habitat enhancement projects have been implemented in the YHT beginning in 1986 (reviewed by Gunson 1997). From 1987 to 1990, 3.25 km² of shrub-encroached grasslands were mowed during July to reduce shrub (primarily bog birch) encroachment and 1.78 km² of the mowed area was also fertilized one time. Shrub-mowing has been standard ranch policy since 1982, with an average of 0.25 km² mowed/year on a rotational basis during June–August (R. Smith, Parks Canada, Ya Ha Tinda Ranch, personal communication). In 1990, 0.33 km² of shrub-encroached grasslands in WMU 416 were also mowed. In 1988, 3.16 km² of mature conifer adjacent to the winter range was logged and seeded with nonnative grasses to enhance elk winter forage. We expected an elk response from fertilizing, mowing, and logging because of demonstrated short-term increases in grass production (reviewed by Morgantini 1995). Similar to fire, we used cumulative area of treated habitats to examine effects of winter habitat enhancements on elk (Table 2).

The number of horses pastured on the YHT ranch during winter (Nov–May) has averaged 150 until recently when numbers have declined <100 (Table 2). Horses have been fed hay (*Agrostis–Dactylis–Phleum* spp. mix) during late winter (Feb–Apr) since at least the late 1970s (Parks Canada, unpublished data), and elk have access to hay provided for horses. Despite scant quantitative data, hay feeding increased since the early 1990s when overgrazing concerns resurfaced, accompanied with an increased frequency of hay depredations by elk (L. Morgantini, University of Alberta–Edmonton, and E. Bruns, Alberta Fish and Wildlife, Rocky Mountain House, personal communication).

Wolves were extirpated throughout all of the Canadian Rockies in the 1950s by poisoning and trapping (Gunson 1992), were considered rare during 1977–1980 (Morgantini 1988), but had naturally recovered by the mid-1980s (Paquet 1993). Currently 30–50 wolves in 4–5 packs overlap the YHT elk population (Hebblewhite 2006). Winter wolf numbers have been surveyed in the BNP portion of the study area through radiotelemetry or winter snowtrack

surveys since the mid-1940s (Table 2; reviewed in Hebblewhite 2006). Unfortunately, similar wolf trend data do not exist for adjacent provincial areas. Despite the potential for effects of harvest in Alberta, Alberta population trends should be coupled with wolf numbers inside BNP because all BNP wolf packs use adjacent Alberta lands (Callaghan 2002). For example, average 100% annual wolf minimum complex polygon territory size in our study was 1,229 km² ($n = 5$; Hebblewhite 2006), indicating the large spatial scales involved with wolf populations. Thus, we assumed wolf population trends in adjacent Alberta areas were the same as in BNP, especially in regard to recovery from extirpation during the duration of the study.

We included effects of summer precipitation (following Portier et al. 1998) and winter severity (Hebblewhite 2005) in population models. We obtained total June–August precipitation (mm) from Environment Canada for Blue Hill tower 20 km southeast of YHT for 1972–2004 (Table 2). We used the North Pacific Oscillation (NPO) climate index (Trenberth and Hurrell 1994) as an index of winter severity for elk (Hebblewhite 2005; available from <<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>>).

Elk Population Dynamics

Because up to 90% of the regional elk population winters in WMU 418 (YHT; Hebblewhite 2006), we considered WMU 418 winter counts of elk as representative of the YHT elk population. We determined population growth rate (r_t) of elk wintering in WMU 418 from aerial counts and adjusted for relocation and harvest by

$$r_t = \ln[(N_{t+1} + H_{t+1}) / (N_t - LH_t)],$$

where r_t is adjusted elk population growth rate, H_{t+1} is the number of elk “removed” (harvested) before winter surveys during year $t + 1$, and LH_t is the number of elk “removed” (late-season hunts and translocated elk) during year t after population surveys (Merrill and Boyce 1991). The numerator ($N_{t+1} + H_{t+1}$) is the prehunt elk population during N_{t+1} , whereas the denominator ($N_t - LH_t$) is the post-late-hunt/relocation population size during year N_t . Adjusting for elk harvest and relocation approximates population dynamics in the absence of hunting (Taper and Gogan 2002). We assumed no poaching loss, no crippling loss, and additive harvest rates.

We modeled how elk density (N_t), horse numbers, wolf numbers, habitat variables, summer precipitation, and the winter NPO index (Table 2) affected r_t over the 32-year time series. Given the a priori importance of density dependence, we retained elk N_t in all models and assumed linear density dependence. Despite debate regarding density dependence, linear density dependence provides a useful first step in analysis of population dynamics (Sinclair and Caughley 1994). We examined factors at one time lag and included nonlinear climatic effects by including quadratic terms. We tested for the following interactions: 1) NPO and wolf numbers (Hebblewhite 2005), 2) NPO and elk density (Portier et al. 1998), and 3) summer rainfall and elk density (Clutton-Brock et al. 1982). We screened variables for

collinearity >0.5 and developed a set of exploratory candidate generalized linear models (GLMs) of factors affecting elk r_t (Burnham and Anderson 1998). Generalized linear models were of the general form

$$r_t = \ln\left(\frac{N_{t+1}}{N_t}\right) = \beta_0 + \beta_1 \text{elk}N(t) + \beta_2 x_2(t) + \dots + \beta_m x_m(t) + \varepsilon,$$

where $t = 1$ to 32 years, N is population size in year t , r_t = population growth in year t , β_0 is the intercept, $\beta_2 \dots \beta_m$ are coefficients of independent variables $x_2 \dots x_m$, and ε is random error where $\sum(\varepsilon_i) = 0$. We estimated GLMs using the identity link by maximum likelihood estimation in Stata 8.0 (StataCorp 2004). We ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c), and where model selection uncertainty arose, a cutoff of $\Delta AIC_c = 2$ was used to estimate the top model set (Burnham and Anderson 1998). We ranked relative importance of covariates using Akaike weights (ω_i) following Burnham and Anderson (1998:141). In the lexicon of Burnham and Anderson (1998), our analyses were exploratory and meant to reveal insights for further research.

We also examined population models of elk counts unadjusted for harvest [$r_{t-\text{raw}} = \ln(N_{t+1}/N_t)$] to evaluate effects of harvest on population dynamics. We estimated K by solving for N_t when $r_t = 0$ in the harvest-adjusted and raw elk models. We used Akaike weights to select the top model set for r_t and raw $r_{t-\text{raw}}$ and constructed unconditional parameter estimates for coefficients to estimate K (Burnham and Anderson 1998). Comparing estimates of K from r_t and raw $r_{t-\text{raw}}$ models compares the effect of harvest on elk N (Sinclair and Caughley 1994).

Results

Ratio of Migrant to Resident Elk (M:R)

The average M:R observed during population surveys in the early period (12.4; SD = 3.22, $n = 6$) was higher than during the late period (3.0; SD = 1.67, $n = 5$, $t_{6,0.05} = 4.35$, $P = 0.002$). If the M:R had not declined, we would expect 47 residents during the late period, much lower than the average of 246 residents observed (Fig. 2; $\chi^2_1 = 705.1$, $P < 0.0001$). There was slight evidence for capture bias in the M:R ratio between the captured and population estimates ($\chi^2_3 = 7.16$, $P < 0.03$) such that the captured sample had a 6% bias towards residents. Despite this slight bias, the M:R ratio of the collared sample of elk generally was consistent with the population M:R ratio from surveys. In 1977–1980, 0 of 22 collared elk were residents. By 2003–2004, 49% of 79 collared elk were year-round residents (Fig. 3).

Migration Dates

Migration dates were normally distributed, and the average spring migration date of 9 radiocollared female elk monitored in 1978 fell within the range of spring migration dates of 79 female elk during the late period (Z-test, $P = 0.53$). Autumn migration was one month earlier during the late period (Z-test, $P = 0.04$; Table 3).

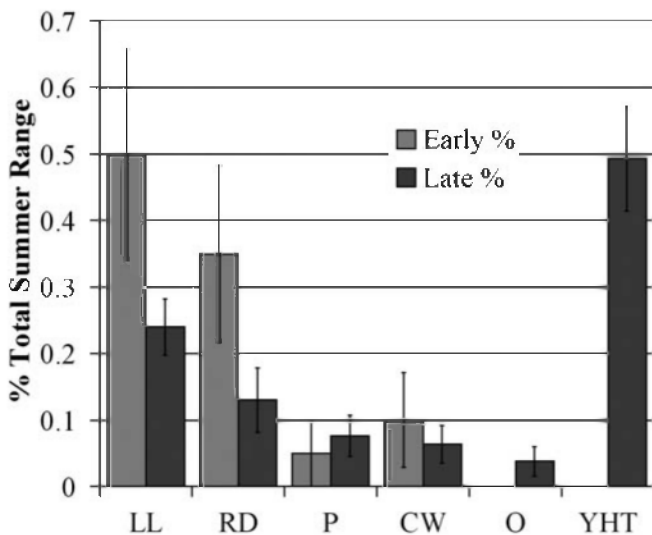


Figure 3. Distribution of radiocollared elk during the early (1978; $n=20$) and late (2002–2003; $n=79$) periods within major summer range areas in Banff National Park, Canada, identified by Morgantini and Hudson (1988). Winter range: LL, Lake Louise; RD, Red Deer; P, Panther; CW, Clearwater; O, Other; YHT, Ya Ha Tinda. Standard errors calculated assuming binomial errors.

Spatial Distribution

From 1977 to 2004, Parks Canada flew 9 surveys, ABFW flew 16 surveys, of which 3 years overlapped, and 4 years had no surveys flown by either agency, resulting in a total of 22 winter surveys. We grouped winter aerial surveys into 3 periods with a balanced 7 surveys each: 1977–1986 (early), 1986–1997 (mid-), and 1998–2004 (late periods; Fig. 4). The 90% adaptive kernel core area for elk locations during winter surveys was 1,418 km² (Fig. 4). A shift in winter elk distribution occurred across the 3 time periods (MRPP $\Delta = 1.49$, $P \leq 0.0001$; Fig. 4), with more elk observed outside BNP near YHT during the latter periods.

Between 1977 and 2004, Parks Canada and ABFW flew 12 and 1 summer surveys, respectively, resulting in 12 years of summer survey data. We grouped surveys into 2 relatively balanced periods with 7 and 5 surveys, respectively, 1977–1986 and 1986–2004 (Fig. 5) to align with winter periods. The 90% adaptive kernel core area for summer observations was 2,708 km² (Fig. 5). Summer elk distributions shifted (MRPP $\Delta = 1.41$, $P = 0.0006$), with noticeable declines of elk in the front ranges of BNP and increases in elk near the YHT (Fig. 5).

Distribution shifts observed in aerial surveys were mirrored by distributions of radiocollared elk (Fig. 3). Spatial distribution of collared elk differed between periods ($\chi^2_1 = 20.2$, $P = 0.003$), with the largest increase in elk occurring in year-round resident elk on the YHT Ranch and the greatest decline in the elk in the Lake Louise and Red Deer areas (Fig. 3).

Population Dynamics

The best r_t models of elk N_t included density dependence and either a negative effect of summer rainfall or cumulative burn area, or a positive effect of winter range enhancement (Tables 4, 5). Of the 3 retained covariates, the effect of fire was most variable and 95% confidence intervals overlapped zero (Table 4). We found high ($r > 0.7$) collinearity between elk N_t and cumulative hectares of winter range enhancement ($r = 0.80$), winter wolf numbers ($r = 0.78$), and number of horses ($r = 0.71$). The high collinearity between elk N_t and winter range enhancement suggests caution is warranted when interpreting the top models (Table 4), although parameter estimates should remain relatively unbiased (Freckleton 2002). Accordingly, we considered models as exploratory. Using the sum of Akaike weights for each variable (Burnham and Anderson 1998:141), we ranked parameters in order of influence on elk population growth rate: summer rainfall ($\sum \omega_i = 0.545$), cumulative burn area ($\sum \omega_i = 0.526$), winter range habitat enhancements ($\sum \omega_i = 0.332$), previous-winter wolf numbers ($\sum \omega_i = 0.141$), the rain \times elk number interaction ($\sum \omega_i = 0.103$), a nonlinear effect of rainfall ($\sum \omega_i = 0.055$), NPO ($\sum \omega_i = 0.023$), NPO \times elk numbers ($\sum \omega_i = 0.004$), hay ($\sum \omega_i = 0.004$), NPO \times wolf numbers ($\sum \omega_i = 0.003$), and a nonlinear effect of NPO ($\sum \omega_i = 0.003$). Other variables had $\sum \omega_i \leq 0.0001$. Based on Akaike weights, only rainfall, cumulative area burned, and habitat enhancements appeared related to elk r_t .

Solving r_t for $N_t = 0$ using unconditional parameter estimates (β_0 and $\beta_i x_i$) for all top models resulted in $K = 1,285$ (95% CI = 1,098–1,471) when adjusted for hunting and management removals, and $K = 954$ (95% CI 779–1,124; Table 5) without adjusting for hunting and management removals (results for r_{t-rdws} are not shown; Hebblewhite 2006). With hunting and management removals, the YHT elk herd was about 25% lower, or 331 fewer elk on average, than without harvest or removals.

Table 3. Midpoints of spring and autumn migration dates of radiocollared elk in the Ya Ha Tinda population for early (1978) and late periods (2002, 2003), Banff National Park, Alberta, Canada.

Period	Year	Spring migration				Autumn migration			
		Date	SD(Date)	Range	<i>N</i>	Date	SD(Date)	Range	<i>N</i>
Early	1978	3 Jun	14.20	17.1	9	5 Nov	8.54	33.1	7 ^a
Late	2002	9 Jun	14.4	12.2	20	30 Sep	25.8	13.5	16 ^a
	2003	1 Jun	13.2	15.6	41	30 Oct	27.2	17.1	38 ^a
Average late		4 Jun	11.5	14.5	61	2 Oct	27.1	16.0	54

^a Autumn *N* is consistently lower than spring *N* due to mortality, radiocollar failure, etc.

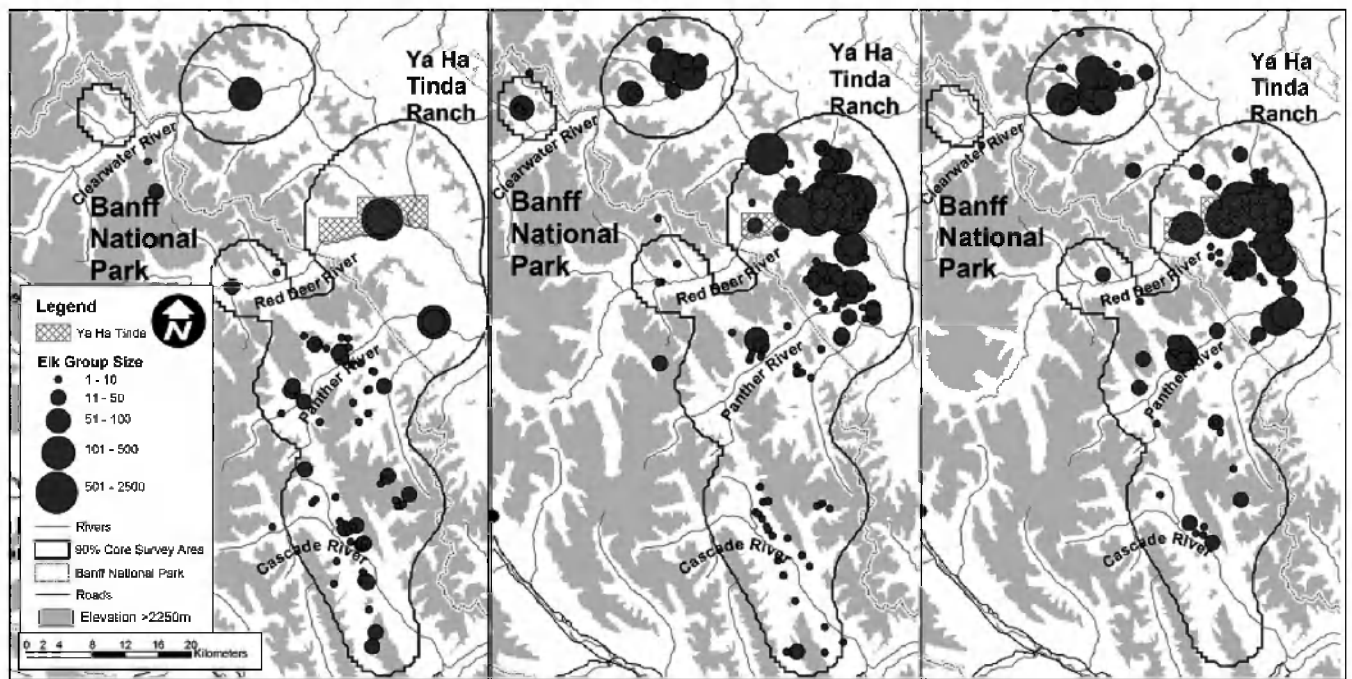


Figure 4. Winter elk distribution (Feb–Mar) during (a) early (1977–1985), (b) mid- (1986–1994), and (c) late (1995–2004) study periods in the Ya Ha Tinda elk population, Banff National Park, Alberta, Canada. The area within which 90% of all aerial observations occurred is shown in the outline. Number of surveys flown per period was equal.

Evaluating Predictions

Evidence from both our hypothetico-deductive framework and population dynamics models suggest observed trends in M:R ratio and population dynamics were consistent with predictions of hypotheses 4, 6, and 8, namely, winter range enhancements, habituation due to hay feeding, and a wolf protection gradient in BNP (Tables 1, 4). However, we could not rule out potential effects of elk relocation (Table 1: H2). Observed elk population trends were opposite the predicted effects of elk harvest, prescribed burning, or horse numbers (Table 1: H1, H3, and H5). Migratory changes also were opposite of predictions if migration reduced wolf predation relative to residents (Table 1: H7). Our population models revealed that only elk N_t , prescribed burns, summer rainfall, and perhaps habitat enhancements (Table 5) affected elk r_t .

Discussion

Our comparison of migratory and population dynamics of the YHT elk herd strongly suggests migration behavior has changed dramatically since the 1970s. The proportion of the population migrating into BNP declined by approximately 75%, and migrant elk now return to the winter range almost one month earlier. These changes cannot be explained by changes in average N_t between the early ($N_t = 608$) and late ($N_t = 917$) periods because M:R declined as N_t increased. The shift in elk distribution was most pronounced from the front ranges of BNP to the YHT in winter, and a corresponding increase from <30 elk in 1977 to >300 elk summering on YHT during 2002–2004 (Fig. 4). While the increase in resident elk occurred during a period of general

population growth, the increase at YHT in summer was greater than expected due to population growth rate alone. Therefore, despite small sample sizes of collared elk during the early period, changes in collared and population samples' M:R ratio and distribution revealed the same trends of declining migration and distribution shifts to year-round residence on the winter range.

Our management hypotheses predictions that were the most consistent with changing migratory behavior were those benefiting resident over migrant elk. These included winter range enhancement, access to hay, and possibly wolf avoidance of the YHT during summer. Resident elk would have benefited from winter range enhancements year-round by summering on improved ranges without migrating. The importance of summer nutrition to elk condition and reproduction is now well documented (Cook et al. 2004). Winter range enhancements may have made winter ranges more nutritious during summer than high-elevation summer ranges, given trade-offs with wolf predation risk (Hebblewhite 2006). While elk feeding on hay during winter may provide energetic benefits, we believe an important effect of hay feeding is as an attractant that leads to elk habituation to humans and loss of traditional behavior (Burcham et al. 1999, Smith 2001, Klopppers et al. 2005). Habituation to humans from hay feeding also would benefit elk in wolf avoidance of human activity on the winter range. Numerous studies have documented carnivore avoidance of high human activity (e.g., Theuerkauf et al. 2003). In BNP the town site created a predation refuge that enhanced elk survival and recruitment (Hebblewhite et al. 2005), leading to migratory declines. While human use may be lower at the

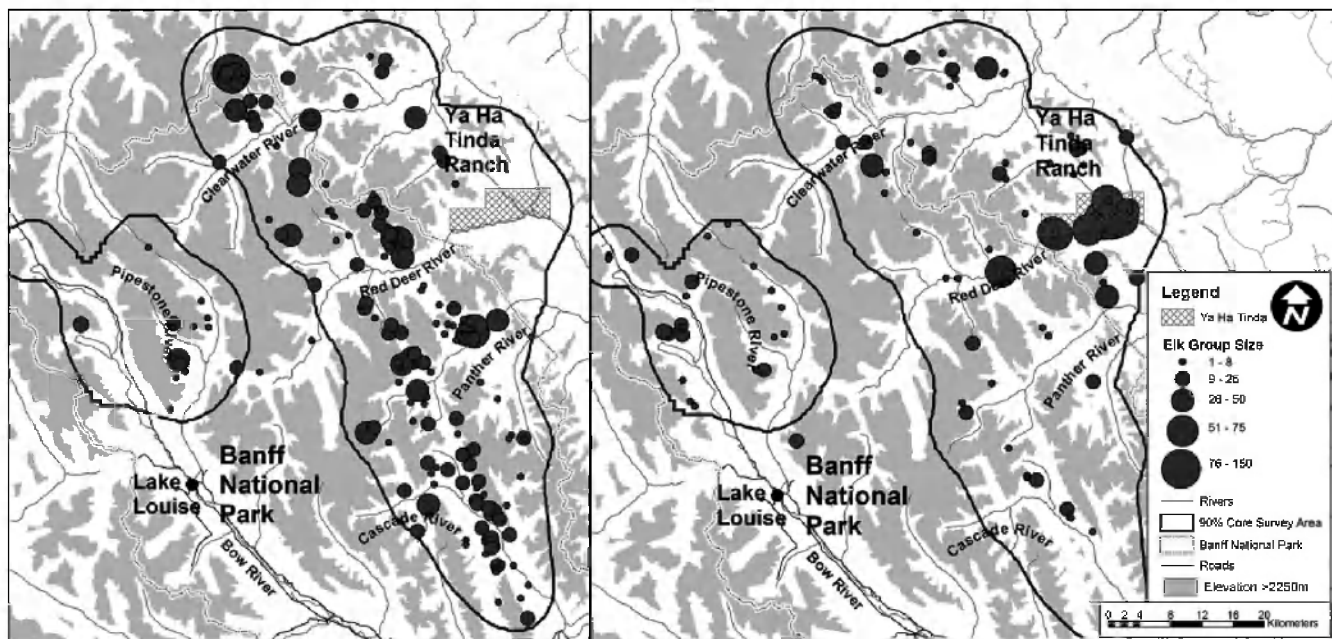


Figure 5. Summer elk distribution of elk (Jul–Aug) during (a) early (1977–1986) and (b) late (1986–2004) study periods in the Ya Ha Tinda elk population, Banff National Park, Alberta, Canada. The area within which 90% of all aerial observations occurred is shown in the outline. Number of surveys flown per period was equal.

YHT than in BNP, direct human-caused wolf mortality from legal hunting and trapping 10 months of the year and some illegal killing during the rest of the year (Hebblewhite 2006) may reinforce wolf avoidance of human activity (Theuerkauf et al. 2003) and foster development of predation refugia, even if human use is lower than in the BV.

In contrast to research elsewhere on elk and fire, we found little evidence that large prescribed fires were effective at increasing migratory elk numbers. In fact, Front Range elk herds that had access to the largest prescribed burns within BNP declined the most, and the effect of fire on population growth was weakly negative, not positive as predicted. Our results may relate to how we measured effects of burning using a cumulative area burned following White et al. (2005). Further, it was difficult to completely isolate effects of burning in our study because the amount of area burned was correlated with declining elk and increasing wolf populations. Despite these caveats, however, we propose the hypothesis that in the presence of wolf predation, effects

of fires are weaker or even negative on elk (White et al. 2005). Almost all previous studies demonstrating positive effects of fire on elk populations occurred in the absence of wolf predation (e.g., Taper and Gogan 2002). Our results at least suggest an interaction between predation by wolves and habitat restoration through fire that has important management implications for ecosystem management in national parks (White et al. 1998).

We suggest the hypothesized demographic benefits of migration (Bergerud et al. 1984, Fryxell et al. 1988; Table 1: H7) may not exist for migrants in the YHT elk herd: by all counts, residents seem to be doing relatively better. In further support, during the 1980s elk resided along the front-range areas of BNP during winter. However, by 2000 wintering elk populations within these areas had declined or shifted to the YHT. While these trends support the existence of a predation refugia, a comparison of wolf predation on resident elk relative to forage trade-offs is required to empirically test for this effect (Hebblewhite 2006). In the absence of experimental approaches, other

Table 4. Population growth rate (r_t) model selection for the Ya Ha Tinda elk population, Alberta, Canada, winters 1970–2004. Following Burnham and Anderson (1998), we report R^2 from generalized linear models, N , K , log-likelihood (LL), ΔAIC_c (AIC_c = Akaike's Information Criterion adjusted for small sample size), and AIC weights. We only report models within 0–2 ΔAIC_c .

Model rank and structure	R^2	N	K	LL	ΔAIC_c	AIC weight
1: Elk N^a + Rain b	0.33	25	3	7.979	0	0.163
2: Elk N + Burn c + HE d	0.35	25	4	9.244	0.325	0.139
3: Elk N + HE	0.33	25	3	7.644	0.669	0.117
4: Elk N + Burn	0.28	25	3	7.344	1.268	0.087

^a Elk N is the postharvest elk N_t .

^b Average summer rainfall (mm) measured at Blue Hill tower, 20 km southeast of Ya Ha Tinda.

^c Cumulative area burned (km 2).

^d Cumulative area affected by winter range habitat enhancements (km 2).

Table 5. Model-averaged parameter estimates and unconditional SEs for the top harvest removal-adjusted r_t elk population growth rate models for the Ya Ha Tinda elk herd, Alberta, Canada, 1970–2004.

Parameter	r_{t-adj} Model	
	β	SE
Intercept	0.440*	0.0904
Elk N_t^a	−0.00034*	0.000045
Rain ^b	−0.00034*	0.000127
Burn ^c	−0.0009	0.0027
Habitat enhancement ^d	0.0154	0.0144

^a Elk N_t is raw elk count in r_{t-raw} model, and postharvest elk count in the r_t model.

^b Average summer rainfall (mm) measured at Blue Hill Tower, 20 km southeast of Ya Ha Tinda.

^c Cumulative area burned (km²) in Banff National Park.

^d Cumulative area of Ya Ha Tinda winter range enhancement (km²).

* Parameter estimates are statistically significant at $P = 0.05$.

tools, such as resource selection functions (Boyce and McDonald 1999), landscape-linked simulation models (Turner et al. 1994), or habitat-linked demographic studies (Johnson et al. 2004), will be required to understand the mechanisms of how predation risk and habitat enhancement interact to influence migratory behavior.

An important management factor not directly tested was one of the most pervasive and difficult to quantify impacts: the effects of human recreation on elk behavior. In the 1970s, Morgantini and Hudson (1979) documented displacement of resident elk on the YHT by motorized use, and motorized human use was restricted in 1986. Recreational activity is now predominantly equestrian-based, which appears to disturb elk less at YHT despite overall increases in human use (M. Hebblewhite, personal observation). Increased human activity, equestrian-based or otherwise, combined with direct human-caused wolf mortality, may repel wolves (Theuerkauf et al. 2003), creating predation refugia (White et al. 1998). Further study of interactions between humans, wolves, and elk on the YHT winter range is needed to confirm whether refugia are leading to reduced migration and whether a refuge is spatial (i.e., Banff townsite; Hebblewhite et al. 2005) or only temporal (e.g., Theuerkauf et al. 2003). As an immediate management implication, aversive conditioning similar to what has been used on elk in the Banff town site (Kloppers et al. 2005) may be necessary to counteract potential predation refugia at the YHT.

The only climatic effect we found was that increased summer rainfall decreased elk r_t , similar to findings of Clutton-Brock et al. (1982). Increased precipitation during June–August often produces snow in the Rocky Mountains and may delay spring plant phenology critical for calf survival and population dynamics (Post and Klein 1999). We speculate the main effect of rainfall on elk r_t may be through reduced calf survival during wetter, colder summers because of the frequency of spring and summer snowfall during wetter summers (Holland and Coen 1983). Winter severity, measured by the NPO, also was unrelated to r_t at $t = 0$ –2 lags. Nearby in the BV, severe winters interacted with

high densities to reduce r_t because the rate at which wolves killed elk increased with winter severity (Hebblewhite 2005). Although the NPO correlates strongly with climate on the eastern slope of the Rockies (Trenberth and Hurrell 1994), azonal climatic conditions characterizing YHT (Morgantini 1995) may have weakened the climatic signature of NPO. Alternately, because the population did not spend much time near K, density–climate interactions may have not occurred.

Our population models also have important implications for long-term controversies surrounding range management at the YHT. We found our assumption of simple linear density dependence was warranted, similar to elk studies elsewhere (e.g., Clutton-Brock et al. 1982, Merrill and Boyce 1991, Lubow and Smith 2004) and estimated carrying capacity (K) based on this density dependence. In comparison to studies elsewhere (Merrill and Boyce 1991, Lubow and Smith 2004), our estimates of K represent ecological carrying capacity with predation rather than food-based K (Sinclair and Caughley 1994). Hunting and relocations reduced long-term N by an average of 22% from approximately 1,285 to approximately 985, closer to sustainable range capacity assessments of K (e.g., AGRA Earth and Environmental 1998). With or without hunting or relocations, long-term equilibrium for the population is toward an N well below the maximum observed number of elk of approximately 2,200. This peak in elk numbers occurred after a series of intermediate precipitation summers, and immediately after fires in BNP and winter range enhancements, and may represent a short-term overshoot of K. In this context, elk management (hunting and relocation) was effective at reducing elk N_t closer to the 1,000 elk recommended based on range assessments for threatened rough fescue conservation (McGillis 1977, AGRA Earth and Environmental 1998). However, at the time range assessments were done, 170–200 horses were wintered at YHT. With recent declines of wintered horses at YHT, it may be worthwhile revisiting range assessments for conservation of threatened fescue grasslands (McInenely 2003).

Differences in resource management policies between federal and provincial agencies across jurisdictional boundaries have facilitated creation of spatial gradients in predation risk and habitat that appear to favor resident elk over migrants. National park policies protect wolves, while provincial policies include liberal wolf harvests to promote elk population goals (Gunson 1997). Inside BNP, management seeks to reduce the negative effects of human recreation (Parks Canada 1997), while the province of Alberta has a more liberal recreation policy for the YHT area (Anonymous 1986). Direct wolf mortality and indirect wolf avoidance of higher human activity at YHT are, therefore, emergent properties of the present transboundary management policy framework. Similarly, Parks Canada seeks to restore long-term ecological conditions through application of prescribed fire to elk summer ranges (White et al. 1998), while the Alberta government had a more

conservative forest fire suppression program, albeit with a growing prescribed fire program. Alberta provincial habitat enhancement policy has instead been focused on elk winter range enhancement, whereas Parks Canada's main objectives for the winter range have been horse grazing and hay feeding (Parks Canada 1987). These contrasting management objectives pose a significant difficulty to development of a common interest approach to the transboundary management of the YHT elk herd (Clark et al. 2000). Historically, there was been little effective coordination of management activities across the park boundary, though recent coordination efforts should be continued and strengthened (e.g., Parks Canada 2002). For example, the Bighorn cutblocks and the prescribed fire programs were implemented by provincial and federal agencies without regional assessment of their effects on the YHT elk herd. We contend that transboundary management must be coordinated through development of a common interest approach, such as maintaining migration across the spatial extent of this elk herd (Clark et al. 2000).

Transboundary management of migratory elk herds will be increasingly important because the factors that changed migration of the YHT elk herd occur elsewhere across western North America (e.g., White and Garrott 2005). Our analyses indicate that isolating factors responsible for migratory changes with certainty will be difficult in complex management settings. We suggest there is sufficient evidence to indicate that recolonization by wolves, winter range habitat enhancements, and habituation to hay have contributed to migratory change. Therefore, these factors merit primary consideration in future management of the YHT elk herd. With recovering wolf populations present or imminent in many areas of western United States, many elk herds will face this new factor as an influence on migratory behavior. Park and wildlife managers should be alert for migratory changes in elk populations, given the important ecosystem ramifications of migration and the implications of changes in migration for park management. For example, in BNP wolf and grizzly bear population viability ultimately

depend on the density of elk as their primary prey (Carbone and Gittleman 2002) and are thus dependent on continued transboundary migrations. Our research provides an illustration of the vital role that areas outside of protected areas have in ecosystem management of national parks (Groom et al. 1999). National parks with transboundary populations of migratory ungulates must increase cooperative management with adjacent agencies to ensure key park processes are maintained.

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