



0 Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs 53

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Partial migration is widespread in ungulates, yet few studies have assessed demographic mechanisms for how these alternative strategies are maintained in populations. Over the past two decades the number of resident individuals of the Ya Ha Tinda elk herd near Banff National Park has been increasing proportionally despite an overall population decline. We compared demographic rates of migrant and resident elk to test for demographic mechanisms partial migration. We determined adult female survival for 132 elk, pregnancy rates for 150 female elk, and elk calf survival for 78 calves. Population vital rates were combined in Leslie-matrix models to estimate demographic fitness, which we defined as the migration strategy-specific population growth rate. We also tested for differences in factors influencing risk of mortality between migratory strategies for adult females using Cox-proportional hazards regression and time-varying covariates of exposure to forage biomass, wolf predation risk, and group size. Despite higher pregnancy rates and winter calf weights associated with higher forage quality, survival of migrant adult females and calves were lower than resident elk. Resident elk traded high quality food to reduce predation risk by selecting areas close to human activity, and by living in group sizes 20% larger than migrants. Thus, residents experienced higher adult female survival and calf survival, but lower pregnancy and calf weights. Cause-specific mortality of migrants was dominated by wolf and grizzly bear mortality, whereas resident mortality was dominated by human hunting. Demographic differences translated into slightly higher (2–3%), but non-significant, resident population growth rate compared to migrant elk, suggesting demographic balancing between resident strategies during our study. Despite statistical equivalence, our results are also consistent with slow long-term declines in migrants because of high predation because of higher wolf-caused mortality in migrants. These results emphasize that migrants and residents will make different tradeoffs between forage and risk may affect the demographic balance of partially migratory populations, which may explain recent declines in migratory behavior in many ungulate populations around the world.

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Migration is thought to have evolved as a fitness-maximizing strategy in the face of temporal and spatial variation in resources (Swingland and Greenwood 1983, Boyce 1991). By migrating, animals track fluctuating forage resources over large areas (Swingland and Greenwood 1983) and can escape regulation by predators (Fryxell et al. 1988). Partial migration, where some individuals migrate and some individuals forego migration (Chapman et al. 2011) may provide equal fitness under some circumstances (Lundberg 1988). Much of our knowledge of partial migration comes from studies of passerines (MacArthur 1959, Lundberg 1988, Boyle 2011, Nilsson et al. 2011). However, partial migration also is common in ungulates, including elk and red deer *Cervus elaphus* (Woods 1991, Mysterud et al. 2011), moose *Alces alces* (Ball et al. 2001, Andersen 1991), mule deer *Odocoileus hemionus* (Nicholson et al. 1997), roe deer *Capreolus capreolus* (Cagnacci et al. 2011), white-tailed deer *Odocoileus virginianus* (Forbes and Theberge 1995), and wildebeest *Conochoaetes taurinus* (Fryxell et al. 1988). This is somewhat of an conundrum in ungulates because most of the literature on ungulate migration shows substantial benefits from migration (Bergerud et al. 1984, Fryxell et al. 1988). This poses the question of why are many ungulate populations partially migratory?
In any population, partial migration is thought to be maintained by some form of demographic balancing between the two migratory strategies under several different mechanisms (Lundberg 1988, Kaitala et al. 1993). First, animals can adaptively switch between migrant or resident strategies as population density, the frequency of each strategy changes, or with changing resource abundance (Lack 1968). Second, animals can adopt a state-dependent migrant or resident strategy dependent on their age or body condition (Adriaensen and Dhondt 1990, Perez-Tris and Telleria 2002). These first two mechanisms are both individual-based mechanisms where one strategy may end up making the ‘best of a bad situation’ (Adriaensen and Dhondt 1990). The third mechanism is could be demographic balancing at the population-level, where individuals are migrant or resident, but proportions are fixed at the population level by density-dependent fitness balancing between strategies (Lundberg 1988). In ungulates, high fidelity to migratory strategies

0 with little evidence for state- or age-dependence (Nicholson
 et al. 1997, Van Dyke et al. 1998) indicates maintenance
 of partial migration in ungulates consistent with popula-
 tion-level demographic balancing. In contrast to songbirds
 (Swingland and Greenwood 1983), few studies have found a
 5 strong fixed genetic basis for migration in ungulates (Bolger
 et al. 2008; but see McDevitt et al. 2009). Where migration
 has been shown to improve access to forage or reduce preda-
 tion risk (Fryxell et al. 1988, Mysterud et al. 2002), partial
 migration in ungulates would be maintained where residents
 10 minimize the relative demographic costs of foregoing migra-
 tion, even if only a low frequency of residents is maintained
 in the population (Fryxell et al. 1988). In contrast, loss of
 migration would be expected where residents could make
 risk–forage tradeoffs to reduce risk and achieve high forage
 15 on winter range year round (Hebblewhite and Merrill 2009),
 or alternately, by making life-history tradeoffs between
 adult survival and reproduction (Pulliam 1989). Given
 widespread declines of migratory behavior in ungulate popu-
 lations worldwide (Berger 2004, Bolger et al. 2008), there
 20 is a growing need to understand the demographic mecha-
 nisms of declines and whether they result from a shifting
 demographic balance to resident strategies.

The purpose of this study was to assess the comparative
 demography of migratory and resident strategies of a par-
 25 tially migratory ungulate herd to evaluate the mechanisms
 of changes in the ratio of migrants to residents. We focused
 on a partially migratory elk population that winters adja-
 cent to Banff National Park (BNP) in the Canadian Rock-
 ies. Over the past 20 years, the proportion of residents in
 30 the population has increased suggesting the demographic
 trends were in favor of residents (Hebblewhite et al. 2006).
 Previously, we have shown that migration to high elevation
 summer ranges in BNP increased access to high forage qual-
 ity and reduced exposure to predation risk (Hebblewhite et
 35 al. 2008, Hebblewhite and Merrill 2008). In contrast, resi-
 dent elk experienced lower forage quality and higher poten-
 tial predation risk, which they avoided by using fine-scale
 refugia caused by wolf avoidance of humans (Hebblewhite
 et al. 2005, Hebblewhite and Merrill 2008, 2009). While
 40 the resource selection strategy of resident elk appeared to
 compensate for giving up the forage benefits of migration,
 whether this translated to demographic differences driving
 changes in migration at the population-level was unknown.
 Therefore, we compared the demography of the two migra-
 45 tory strategies to test the hypothesis that demographic
 benefits from resource selection for refugia by resident elk
 compensated for poorer forage, equalizing resident and
 migrant elk fitness, thereby maintaining partial migration
 in this population. We did not expect facultative switching
 50 between strategies (Hebblewhite 2006), nor a strong genetic
 basis for migration because of the recent genetic bottleneck
 and reintroduction history of elk (Hicks et al. 2007).

To test this hypothesis, we compared vital rates and
 population growth rate (λ) between migrant and resident
 55 strategies, and evaluated the effects of exposure to predation
 risk, forage, their interaction, and elk group size on adult
 survival (Frair et al. 2007). We predicted that survival would
 be decreased by exposure to predation risk and increased
 by exposure to high forage quality year-round, and that
 60 these differences would be consistent with resource selection
 differences between migratory strategies (Hebblewhite and
 Merrill 2009). Vital rates were combined in Leslie matrix
 models to compare relative demographic fitness between
 strategies of adult females, which we defined as strategy-
 specific population growth rate, λ (Caswell 2001).
 65 We used the ratio of migrant and resident λ 's to estimate the
 relative growth differential between strategies, equivalent to
 the rate of change in the migrant to resident (M:R) ratio in
 the population (Kaitala et al. 1993).
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75 Methods

Study area

The study area lies on the eastern slopes of the rugged Cana-
 dian Rockies Ecosystem in and adjacent to Banff National
 Park (BNP), Alberta, Canada. The study was conducted from
 February 2002 to June 2005 in a 7000 km² area defined by
 the movements of the Ya Ha Tinda (YHT) elk population.
 80 Elk are the most abundant ungulate and the dominant prey
 of wolves, which are in turn elk's main predator (Hebble-
 white et al. 2004). Other prey species, in approximate order
 of relative abundance, include bighorn sheep *Ovis canadensis*,
 mule deer *Odocoileus hemionus*, white-tailed deer *O.*
 85 *virginianus*, mountain goats *Oreamnos americanus*, moose
Alces alces, and, until recently (Hebblewhite et al. 2010), a
 remnant herd of 5–8 mountain caribou *Rangifer tarandus*.
 Other predators include grizzly bears *Ursus arctos*, black
 bears *Ursus americanus*, cougars *Felis concolor*, wolverines
 90 *Gulo gulo*, and coyotes *Canis latrans*. Almost the entire elk
 (95%) population winters at the YHT winter range. During
 summer migrants move to summer ranges 20–60 km distant
 while residents remain on the YHT year-round. Historically,
 the proportion of migrants in this population approached
 95 100%, but recently has declined to nearly 50% concurrent
 with declines from 2200 to 1000 elk (Hebblewhite et al.
 2006). While heavy bull harvests have been a historic fea-
 ture of elk management, a short-term female hunting sea-
 son of ≤ 30 female elk occurred from 1999 to 2003 (AB
 100 Fish and Wildlife, unpubl. data) partially during our study.
 For more details about the study area see Hebblewhite et al.
 (2006).

Elk capture and monitoring

105 We captured 352 elk during winter (15 January to 31
 March) from 2002–2004 at the YHT winter range (Univ. of
 Alberta Animal Care Protocol no. 353112) using two cor-
 ral traps baited with alfalfa hay; 11 elk were captured via
 110 helicopter netgunning, and all elk were handled without
 chemical immobilization. Of these 352 elk we outfitted 109
 female elk (\geq yearling age) with VHF or GPS radiocollars
 (LOTEK 2200 and 3300 collars) without knowledge of their
 migratory behavior. In total we deployed 32 GPS and 120
 115 VHF collars, with some elk wearing both types consecu-
 tively. Female elk were aged into four age classes based on
 tooth eruption, body weight, and capture history (i.e. those
 captured as calves); calves, yearlings (<1.5 to 2.5 years),
 subadults (<2.5 years) and adults (>2.5 years). Body mass
 of elk was recorded using a livestock scale. We monitored
 121



0 GPS and VHF elk aerially or from the ground a mean and
 median of once every 9.0 (SE = 11.13) or 6.0 days, respec-
 tively, until death, emigration, or the end of the study. GPS
 collar locations collected every 2-h were re-sampled to 6-day
 5 intervals equivalent to VHF telemetry for survival analy-
 ses to ensure consistent sampling between migrant strata.
 Mean VHF location error was 218 m, 50% of GPS locations
 were within 34 m, and 95% within 113 m (Hebblewhite
 et al. 2007). Habitat-induced GPS bias was low enough to
 not influence habitat analyses (<10%, Frair et al. 2004,
 10 Hebblewhite et al. 2007). We defined migrant and resi-
 dents by identifying movements between non-overlapping
 seasonal summer ranges with VHF and GPS telemetry
 (Craighead et al. 1972). We estimated between-year switch-
 ing rates between migratory strategies for 2002–2005 based
 15 on elk with known migratory history.

Adult female survival

20 Radiocollared elk mortalities were investigated 5.2
 (SE = 7.98) days after detecting VHF mortality signals, and
 we ascribed cause of death to predator (wolf, grizzly, other),
 human harvest, disease, or unknown causes following sys-
 tematic criteria (Hebblewhite 2006). Deaths within 1 month
 of capture (n = 2) were considered capture myopathy and
 25 censored. All but two mortalities (hunter kills) had known
 mortality date and location, and for these two we used the
 last known location in Cox-survival modeling. We used non-
 parametric Kaplan-Meier (K-M) survival analysis (Therneau
 and Grambsch 2000, Cleves et al. 2002) to estimate annual
 30 survival rates of residents and migrants between January
 2002 and June 2005 within biological years 2003 and 2004
 (Table 1). Differences between migrant and resident survival
 rates were tested using the log-rank test (Cleves et al. 2002),
 and average annual cause-specific mortality rates calculated
 35 from K-M estimators.

Factors influencing survival

40 We modeled risk factors influencing annual adult female
 survival using the semi-parametric Cox-proportional hazards
 model (Cox 1972, Andersen and Gill 1982, Therneau and
 Grambsch 2000) following:

$$h(t|x_j) = h_0(t) \exp(\mathbf{X}_j \beta_x + \epsilon) \quad (1)$$

45 where $h(t|x_j)$ is the hazard for the j th elk, $h_0(t)$ is the base-
 line hazard, and $\mathbf{X}_j \beta_x$ is the vector of risk covariates, \mathbf{X}_j
 for elk j and their coefficient, β_x . We set the time origin as
 calendar time following Fieberg and DelGuidice (2009).
 50 We tested the proportional hazard assumption for strategies
 and seasons using Schoenfeld residual plots and graphical
 methods (Therneau and Grambsch 2000, Cleves et al. 2002).
 If models violated the proportional hazards assumption, we
 attempted to meet assumptions by transformation, adding
 55 time or seasonal covariates (e.g. winter), or stratification (e.g.
 migrant, resident). We assessed covariate fit using Marti-
 n-gale residual plots, and assessed goodness of fit by testing for
 a 1:1 slope between the Cox-Snell residuals and the Nelson-
 Aalen cumulative hazard (Therneau and Grambsch 2000).
 60 We considered an all inclusive set of candidate models

61 consisting of the following four time-varying annual covari-
 ates: herbaceous forage biomass (g m^{-2}), wolf predation risk,
 their interaction, and elk group size. We explored strategy-
 specific effects by interacting these four covariates with a
 65 dummy variable for migrants (1) and residents (0), as well
 as group size and predation risk (Hebblewhite and Pletscher
 2002). We selected the top model using AICc (Burnham
 and Anderson 1998) where the sample size was conserva-
 tively set at the number of deaths (Hosmer and Lemeshow
 1999), and the number of parameters was the number of
 70 covariates + 1 for $h_0(t)$ and + 1 for stratum (Therneau and
 Grambsch 2000).

We used previously developed annual spatial models of
 wolf predation risk and forage biomass to estimate the forage
 and risk at each elk telemetry location for survival model-
 75 ing (see Hebblewhite and Merrill 2007, 2008, Hebblewhite
 et al. 2008 for details of forage and risk models). Briefly,
 exposure of individual elk to wolf predation risk was based
 on multiplying an estimate of large-scale spatial density
 (Hebblewhite and Merrill 2007) by a spatial model of wolf
 80 resource selection functions obtained from GPS-collared
 wolves in all overlapping wolf packs for the elk population
 (RSF, Manly et al. 2002, Hebblewhite and Merrill 2008: see
 also Kauffman et al. 2007 for a similar approach). We mod-
 eled herbaceous forage biomass available for each individual
 85 elk over the growing season (1 May to 15 October 15) using
 a combination of ground-based and satellite remote-sensing
 approaches. Briefly, we estimated herbaceous forage biomass
 at the peak of the growing season (4 August) using stratified-
 random sampling (n = 983 plots) within landcover strata,
 90 and then developed spatial statistical models for peak her-
 baceous biomass. Next, forage growth was spatially modeled
 from the start (8 May) to the end (15 October) of each grow-
 ing season in 16-day intervals using NDVI from MODIS
 95 (Huete et al. 2002). In a GIS, the peak of forage biomass

Table 1. Vital rates of migrant and resident female elk and within-
 population process variance ($\hat{\sigma}^2$ within) estimates used in matrix
 population modeling for the Ya Ha Tinda elk population, Banff
 National Park. Process variance is the average within population
 process variance reported from a review of >40 elk population stud-
 100 ies in Raithel et al. (2006). Yearlings are age 1–2, prime age adults
 3–10, old-age adults 11–14, and senescent adults ages 15+.

Vital rate	Migrants		Residents	
	Parameter estimate	$\hat{\sigma}^2$ within	Parameter estimate	$\hat{\sigma}^2$ within
Calf survival (ϕ)†	0.163	0.025	0.185	0.02
Yearling ϕ ‡	0.849	0.0025	0.865	0.0025
Prime-age ϕ ‡	0.848	0.002	0.875	0.002
Old-age ϕ ‡	0.830	0.002	0.845	0.002
Senescent ϕ ‡	0.695	0.0035	0.707	0.0035
Yearling pregnancy†	0.170	0.0085	0.170	0.0085
Prime-Age Pregnancy††	0.900	0.01	0.830	0.01
Old-age pregnancy ††	0.836	0.0017	0.766	0.0017
Senescent pregnancy ††	0.530	0.0044	0.530	0.0044

†direct estimates from this study.

‡estimated based on overall adult female ϕ from this study decom-
 posed into the different adult female age-class survival rates based
 on (Houston 1982) following (Raithel et al. 2006).

††prime-age and yearling pregnancy rates were estimated from this
 study, and old-age and senescent rates were estimated based on
 prime-age following (Raithel et al. 2006).

0 and growing season models were combined to create 16-day 'maps' of forage availability between 8 May and 15 October, and overwinter forage decline was modeled by linearly interpolating graminoid-only biomass until the start of the next growing season. In contrast to predation, which is event driven, survival consequences of forage exposure likely occur over longer temporal scales (Cook 2002). Therefore, we calculated an index to cumulative forage biomass exposure for each elk as the running-mean value of exposure to forage using graminoid biomass estimates for each elk reset to 0 each year on 1 June to mimic annual cycles of body condition in wild ungulates (Cook 2002). Because of the inverse relationship between forage biomass (g m^{-2}) and quality (digestibility) during summer, high forage biomass values index low forage quality (Hebblewhite et al. 2008). The value of forage exposure reflected the nearest 16-day value to the date of observed survival/telemetry location.

We also included group size as a covariate in the Cox-model because previous work showed group size modified predation risk (Hebblewhite and Pletscher 2002). We obtained visual counts of elk group size from 72% of VHF elk observations. For missing observations of group size at the remaining 28% of the VHF observations and all GPS locations, we estimated group size using either: a) the monthly median group size for each strategy, or b) where observations/month was insufficient (≤ 2 , 35% of all elk-months), the median group size was assigned for that month and migratory strategy.

Reproductive rates

We determined late-winter elk pregnancy rates ($n = 141$) for elk captured on the winter range from 2002–2005 using a pregnancy specific protein B (PSPB) assay in elk blood serum (Noyes et al. 1997). Mean pregnancy rates were then analyzed by age-class and year for adults. Logistic regression was used to test for the influence of migrant status and a migrant \times year interaction, while controlling for the effects of year, age-class, weight and capture date.

Elk calf survival

We estimated elk calf survival by resighting calves of collared female elk (Testa 2004, Bonefant et al. 2005) that were known to be pregnant in late winter. We resighted calves with collared females during two 'resighting' periods, summer (1 June – 15 August, mean 15 July), and winter (1 March – 15 May, mean 22 March) in biological years 2003 and 2004. Elk were observed from < 300 m with 45×60 -x spotting scopes or on aerial surveys for an average of 34 (SE = 2.6) minutes each per period (24 min in summer, 48 min in winter). Summer observation time did not differ between migrants (20 min, SE = 2.9) who were more likely to be observed aerially, and residents (28 min, SE = 3.6). Calf presence was noted by observing suckling, grooming, perineal licking or associated movement (Bonefant et al. 2005). Using repeat observations of known status female:calf pairs, we estimated the resighting probability of detecting a calf, given it was alive, as 0.93 (SE = 0.028, $n = 67$ known females with calves). This was similar to Testa (2004)'s resighting rate of 0.96 for moose, and higher than Bonefant et al.'s (2005) 0.81 resighting rate

for red deer. With 2.1 sightings/ resighting period, we had only a 0.014 probability of missing a calf/resighting period. Therefore, we considered calf status (live, dead) as known-fate for survival estimation (Testa 2004). Assuming the false-positive rate was zero, the pregnancy test was considered the initial 'sighting', resulting in three resighting periods and two intervals to estimate survival (Fig. 1). Late-term abortion rate was assumed to be zero similar to Raithel et al. (2006). Survival during the interval from pregnancy testing (4 March) to summer (15 July), therefore, reflected neonatal survival, $\phi_{1(\text{neonatal})}$, from the mean parturition date for elk in our study area (Flook 1970, Woods 1991) of 1 June to 15 July, a 45-day period. Survival during the second interval 15 July to 22 March, a 250-day period, reflected summer and winter survival, $\phi_{2(\text{summer-winter})}$ (Fig. 1). Given that most elk calf mortality occurs during the neonatal period (Barber et al. 2005), we assumed survival for the remainder of the year, from 22 March to 31 May was equal to ϕ_2 , and multiplied $\phi_{1(\text{neonatal})} \times \phi_{2(\text{summer-winter})} \times \phi_{2(22 \text{ March} - 31 \text{ May})}$ to estimate annual survival rates of calves ϕ_{annual} (Fig. 1).

Elk calf survival was modeled using a known fate approach in program MARK (White and Burnham 1999). We included different seasonal survival rates for ϕ_1 and ϕ_2 and group-level covariates for migrant status and year (2003, 2004). Calves of collared females that were not observed in the summer were censored. The top model was selected using AICc (Burnham and Anderson 1998) from a competing set of all possible candidate models including models for constant winter survival between years and strategies based on the shared winter range. We used a bootstrap GOF test to approximate c to correct for overdispersion (White and Burnham 1999). Monthly survival rates were calculated for each survival interval to facilitate comparison. For calculation of monthly and annual survival rates, we used the delta method to derive variance estimates (White and Burnham 1999).

Demographic fitness of migrant and residents

We constructed pre-birth pulse Leslie-matrix models to estimate population growth rates of migratory and resident elk, and tested for demographic fitness balancing using the ratio of migrant to resident rates (Caswell 2001), following similar matrix modeling methods as Raithel et al. (2006). We modeled elk survival in annual time-steps based on vital rates for five age classes; calf (< 1 year-old), yearling (1–2 years), prime-age adult (2–10), old-age adult (10–15), and senescent (> 15). We divided adults into prime-age and old-age to account for survival declines prior to senescence, and we did not truncate the matrix model to enforce senescence by a set age, instead letting survival itself impose the upper limit. Thus we used a 15×15 matrix to model annual vital rates up to 15-years of age, and then senescent animals remained in



Figure 1. 'Mark-resighting' design used for known-fate calf survival estimation. Assuming intrauterine survival = 1.0, The $\phi_{1(\text{neonatal})}$ interval is an average of 45 days, and $\phi_{2(\text{summer-winter})}$ is an average of 250 days. See text for details.

0 the 15th age-class until death (see Hebblewhite 2006 for the
 matrix format itself). Reproduction occurred at ≥ 2 years.
 Calf survival was assumed to be constant between sexes,
 and sex ratio at birth was assumed 50:50. In pre-birth pulse
 models, the top-row of the Leslie matrix is the product of
 5 fecundity and calf survival rates. Fecundity was the product
 of the number of female calves born (sex ratio), intrauter-
 ine survival rate, and pregnancy rate. Elk were assumed to
 bear one young, and because pregnancy was estimated on a
 mean date of 8 March in this study, we assumed late-term
 10 intrauterine survival to be 1 (Raithel et al. 2006). Thus,
 fecundity rate was simply the half the pregnancy rate. This
 approach assumes both strategies were at a similar stable age
 distribution, a challenging assumption for many populations
 (Caswell 2001); however, because we lacked any age struc-
 15 ture data for this population, we had no choice but to adopt
 the stable age distribution assumption. Future studies should
 examine differences in age structure between migrant and
 resident ungulates.

We used data from this study for migrant and resident
 20 age-specific vital rates where possible. Estimates for resident
 and migrant mean annual ϕ_{calf} (calf survival) came from this
 study. However, ϕ_{adult} was estimated only for all elk > 2 years
 old like many studies (reviewed by Gaillard et al. 2000), yet
 age-structure has important effects on ungulate population
 25 dynamics. Therefore, we used Raithel et al.'s (2006) life-table
 approach to decompose the pooled ϕ_{adult} into ϕ_{vly} , $\phi_{\text{prime-age}}$,
 $\phi_{\text{old-age}}$, and $\phi_{\text{senescent}}$ age-class survival rates based on the age
 distribution (13% yearlings, 72% prime-age, 10% old-age,
 and 5% senescent) and survival from Yellowstone National
 30 Park (Houston 1982), which were similar to earlier studies
 in BNP (Flook 1970). Age-class survival rates were calcu-
 lated proportionately from Houston (1982) such that when
 weighted by the age-distribution was equal to the mean
 annual survival rate for both strategies (Raithel et al. 2006).
 35 Results from a simpler, three-stage matrix model (calves,
 yearlings, adults) did not differ from our five-stage model
 (Hebblewhite 2006), so we report the five-stage model to
 enable direct comparisons to Raithel et al. (2006)'s review.
 Pregnancy rates from this study were used to estimate fecun-
 40 dity (F) for F_{vly} and $F_{\text{prime-age}}$, where only $F_{\text{prime-age}}$ differed
 between migrant strategies (see results). $F_{\text{old-age}}$ and $F_{\text{senescent}}$
 were assumed to be the same decline in pregnancy from
 $F_{\text{prime-age}}$ to $F_{\text{old-age}}$ and $F_{\text{senescent}}$ as Raithel et al. (2006).

We calculated population growth rate (λ) and its variance
 45 for each strategy using life-stage simulation analysis
 (LSA) to account for variability in vital rates (Morris and
 Doak 2002). LSA simulates replicate matrix models using
 vital rates drawn at random from a mean and process vari-
 ance. We used mean vital rates for elk in our study as defined
 50 above. However, we did not estimate process variance for
 our three-year study, but used the 'within-study' process
 variance estimates from Raithel et al. (2006) comprehensive
 review of over 50 elk population studies that used the White
 55 method to decompose variance (Morris and Doak 2002).
 This approach assumes similar process variance between
 the mean of Raithel's studies and ours; future analyses with
 long-term data will be required to address this assumption.
 We simulated 1000 replicate matrices from the observed
 60 distribution for each vital rate following Morris and Doak
 (2002) and Raithel et al. (2006). See Hebblewhite (2006)

for full details of the LSA. We tested whether migrant (λ_M) 61
 and resident (λ_R) growth rates, and hence the ratio of M:R,
 were different using a randomization test of the distributions
 of simulated λ from the 1000 simulations (Caswell 2001,
 65 Morris and Doak 2002).

Results

Elk capture and monitoring

70 Of the 120 collared elk used in the survival analysis, 53 (45%)
 were residents and 65 (54%) were migrants. Each elk was
 monitored for a mean of 1.9 years, or 550 days. We moni-
 75 tored 150 elk for a total of at least two migratory seasons. Two
 elk monitored for at least two years switched between migra-
 tory strategies a total of three times (one switched each year of
 the study) for an switching rate of 2.0% elk⁻¹ year⁻¹. How-
 ever, there was no consistent switch from migrant to resident
 80 (two switched from migrant to resident, one from resident to
 migrant), and a net switching rate close to 0%/year.

Adult female survival

85 A total of 39 mortalities occurred during the period from
 2 February 2002 to 30 November 2004 (18 migrant, 21
 residents, Fig. 2). Wolves were the largest source of mortal-
 ity (n = 17, 43%), which occurred year round, followed
 by human harvest (n = 11, 26%), grizzly bears (n = 7,
 19%), and other sources (n = 5, 11%) of mortality includ-
 90 ing coyote, cougar, and disease/starvation. Human harvest
 was comprised of 18% bow hunting, 18% rifle, and 18%
 poaching, and 46% by treaty First Nations. Total monthly
 mortality peaked during June migration (n = 9), driven
 by grizzly bear predation (57%), and during September –
 95 November (n = 11) mortality was driven by wolves and
 human harvest (46% and 36%, Fig. 2). Overwinter mortal-
 ity (November – April, n = 17) was lower than summer
 (May – October)(n = 22), especially without human hunt-
 ing. Mortality causes differed between migrant and residents
 100 (χ^2 -test = 20.82, p = 0.0001, DF = 3). Although there were
 more migrants killed by grizzly bears and wolves, the overall
 significant difference was driven by higher human harvest of
 residents (Fig. 2; G-test χ^2 for harvest p < 0.01).

Average survival rates across the study for residents were
 105 0.840 (SE = 0.032) and 0.862 (SE = 0.035) for migrants,
 and did not differ (log-rank χ^2 -test, DF = 1, p = 0.31, Table
 1, Supplementary material Appendix A1). However, resident
 survival varied between years and was significantly higher
 than migrants in 2002 (log-rank χ^2 -test, DF = 1, p = 0.03)
 110 but lower than migrants in 2003 (log-rank χ^2 -test, DF = 1,
 p = 0.05). Cause-specific mortality rates confirm results of
 Fig. 2 that migrants had higher wolf and grizzly mortal-
 ity, especially, while residents had higher human mortality
 (Table 2). 115

Factors influencing survival

Survival of elk met proportional hazards assumptions for all
 121 covariates including migration status (Schoenfeld residual
 $\chi^2 = 1.77$, p = 0.185, linear Cox-snell partial residual plots),

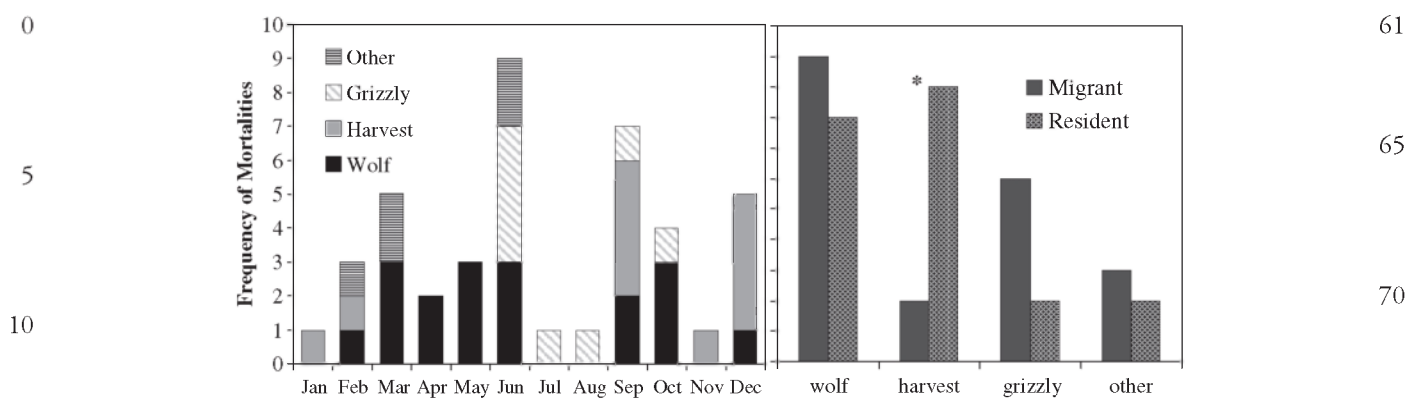


Figure 2. Frequency of adult female elk mortalities by a) mortality cause and b) migratory strategy in the ya ha tinda elk population, february 2002 to november 2004. Significant differences between mortality causes for migratory strategy are marked with an * (see text for details).

therefore we did not stratify models by migration status. Including seasonal (winter, summer) or migratory interactions (e.g. with group size) did not improve any models. The top model was selected with a high degree of certainty ($\Delta AICc = 3.5$ between the first and second ranked models), so we report only this model here (details in Hebblewhite 2006). The top model also showed a reasonable fit to the data ($LR \chi^2 = 9.82$, $p < 0.043$), and showed high predictive accuracy based on the correspondence of the ranked daily hazard and the frequency of deaths (Spearman's $\rho = 0.852$, $p = 0.0015$, $n = 10$ bins, details in Hebblewhite 2006). We present hazard ratios, which are the natural logarithms of the β 's in Eq. 1, where a hazard ratio (HR) $<$ and $>$ 1 implies reduced or increased relative risk of death, respectively. The same covariates occurred in the top model for both migratory strategies; no covariates were retained in the top model were specific to only one migration strategy.

Migrant elk had lower mortality hazard (HR = 0.61), although this was not significantly different from residents (Table 2), similar to log-rank tests of Kaplan-Meier survival rates reported above. Elk mortality hazard decreased (HR $<$ 1) as cumulative exposure to forage increased within a year from June (Table 2). Because the HR for the F \times P interaction was $>$ 1 (Table 2), hazard increased more rapidly in areas of both high forage biomass and predation risk (Fig. 3). Risk of death also decreased with large group size, such that mortality hazard was constant up to groups of \sim 75, after which it declined exponentially (Table 2, Fig. 4). Group size differences were most pronounced in summer (June–Aug) when resident group size averaged 93.1 (SD = 71.4), and migrants 31.2 (SD = 56.1), (Fig. 3), which translated to migrants having \sim 20% higher hazard in summer due to seasonal group size differences alone. In

Table 2. Mean annual cause-specific mortality rates of migrant and resident elk during 2002–2004, Ya Ha Tinda elk population, Banff National Park. SE's calculated via the delta approximation. Harvest includes legal bow and rifle, poaching, and treaty First Nations harvest. Other includes cougar, coyote, and disease.

% Mort	Migrant	Se	Resident	Se
Wolf	0.076	0.010	0.053	0.009
Harvest	0.015	0.004	0.059	0.010
Grizzly	0.046	0.007	0.013	0.004
Other	0.023	0.005	0.013	0.004

contrast, in winter, group sizes were identical, with migrants in groups of 263.2 (SD = 213.2), and residents in groups of 264.3 (SD = 215.8) because migrants and residents lived in mixed groups during this season.

Pregnancy rates

Pregnancy rates varied from 0.66 to 0.98 during 2002–2005 (n total = 78, $n = 12$ to 25 year $^{-1}$ strategy $^{-1}$, Supplementary material Appendix A2). Yearling pregnancy was low at 0.167 (Supplementary material Appendix A2), and we had insufficient sample size to determine differences between strategies. Migrant adults had higher pregnancy rates (0.90, SE = 0.007, logistic regression $\beta_{migrant} = +2.90$, SE = 1.21, $p = 0.001$) than adult residents (0.83, SE = 0.001), except during 2003 (interaction $\beta_{migrant*2003} = -3.43$, SE = 1.82, $p = 0.001$). Of 158 adult females, we determined consecutive pregnancies for 23 elk for two-years, and three of these

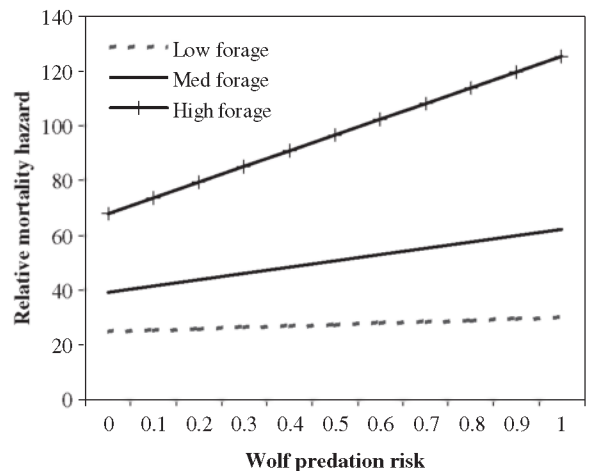


Figure 3. Relative mortality hazard from the top cox-proportional hazards regression model for migrant and resident adult female elk, ya ha tinda elk population, banff national park, alberta, canada, 2002-2004. Relative mortality hazard is estimated from $h(t|x_t) = h_0(t) \exp(\beta x_t)$ at average annual exposure to 5, 25, and 50 g m $^{-2}$ (representative of low, medium and high forage biomass in the study) of herbaceous forage biomass across relative wolf predation risk, averaged across both migrants and residents whose hazards did not significantly differ in the top model. Note that forage quality declines with increasing forage biomass.

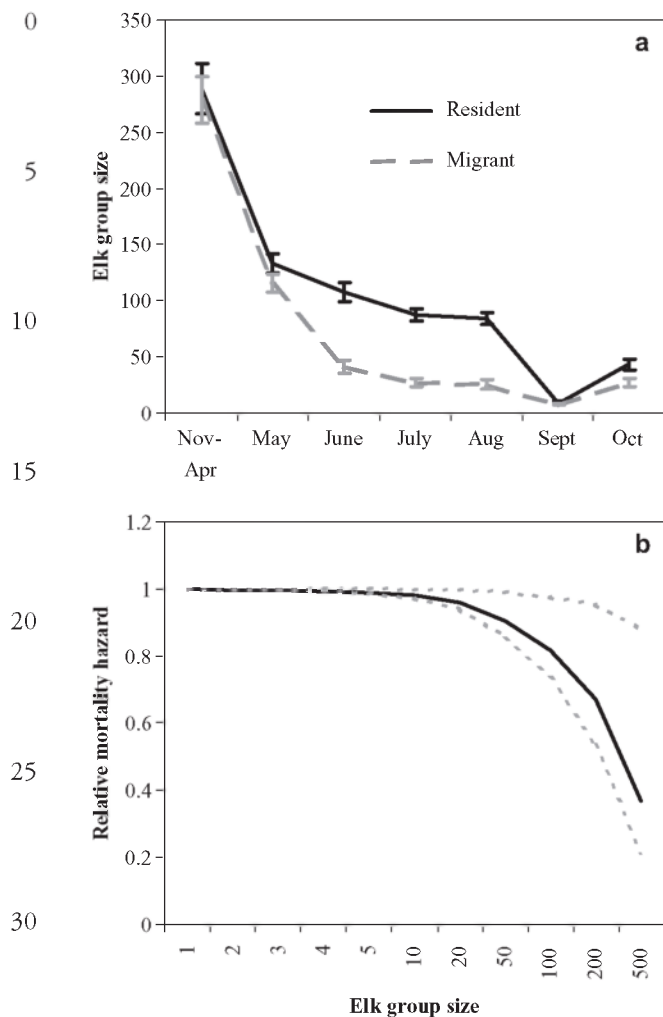


Figure 4. Adult female migrant and resident elk a) seasonal group size relationships (\pm 95% CI) and b) relative mortality hazard (\pm 95% CI) from the top cox-proportional hazards survival models, ya ha tinda elk population, banff national park, alberta, 2002–2004.

elk for three-years. Excluding one female elk that was barren in both years, only 62% ($n = 16$) bred consecutively each year as determined by consecutive sampling. Migrants had slightly higher prevalence of consecutive breeding (68%) compared to residents (57%), but this difference was not significant ($\chi^2 = 5.1$, $p = 0.21$).

Elk calf survival

Survival of 79 calves (33 residents, 46 migrants) was monitored in 2002 and 2003 from pregnancy testing on 8 March to 22 March the following year (Supplementary material Appendix A3, A4). Because $c = 1.504$ was > 1 in the overall bootstrap goodness of fit (GOF) test, we corrected for overdispersion using quasi-likelihood methods (White and Burnham 1999). Given model selection uncertainty in the top model set (Supplementary material Appendix A3) we report here the model averaged (Burnham and Anderson 1998) calf survival by interval for migrant and resident calves (Table 1). Migrant $\phi_{1(\text{neonatal})}$ (0.615) was not statistically

Table 3. Risk factors from the top Cox-proportional hazards model influencing mortality of resident and migrant elk, Ya Ha Tinda elk population, Banff National Park, 2002–2004. Effects are reported as hazard ratio's (βx), and are interpretable similar to odds ratios, with associated SE and p-values.

Risk factor	Hazard ratio $\text{Ln}(e^{\beta x})$	SE	P
Migrant status	0.613	0.191	0.152
Forage (herbaceous biomass:g m ⁻² , annual running mean)	0.957	0.023	0.074
Wolf predation risk (pack-level, unitless)	0.077	0.178	0.11
Forage X wolf predation risk interaction	1.149	0.090	0.077
Group size	0.998	0.002	0.15

lower than neonatal survival for residents (0.697) (Supplementary material Appendix A4). Summer–winter survival, $\Phi_{2(\text{summer-winter})}$ was similar for both migrant and resident elk (0.266 vs 0.265). Annual calf survival rates for migrants (0.163) was also not statistically lower than residents (0.185; Table 1). Survival also did not differ between years (Supplementary material Appendix A4). While these calf survival rates may seem low, and potentially biased because we did not monitor from 22 March to 31 May, they were closely corroborated with low calf:cow ratio's of 0.12 (SE = 0.025), which roughly correspond to calf survival rates expected based on Harris et al. (2008).

Demographic fitness of migrant and residents

vital rates and estimates of process variance used in matrix-models are summarized in Table 1. Accounting for uncertainty in vital rates using in matrix models using life-stage simulation analysis (LSA), the stochastic population growth rate for migrant and resident were $\lambda_R = 0.866$ (SD = 0.105) and $\lambda_R = 0.897$ (SD = 0.145). Both migrants and residents were declining (randomization test for both λ_R and $\lambda_R < 1.0$, $p < 0.05$) at a rate of ~10–12%. However, the 3.3% difference between the stochastic population growth of the two strategies was not statistically different (randomization test $p = 0.36$). Thus, while the ratio of λ_R/λ_R suggested the resident proportion of the population was increasing by 3.3%, uncertainty in this ratio included 1 (randomization test $p = 0.25$).

Discussion

Despite the adoption of vastly different resource selection strategies to avoid predators and obtain forage (Hebblewhite and Merrill 2009), migrant and resident elk realized similar demographic fitness, as indicated by non-significantly different adult female survival (both from log-rank tests and Cox-models) and calf survival, which lead to equivalent population growth rates. Few, if any studies have shown equal demographic fitness of migrant and resident ungulates, although it has been reported for a wide array of other species (American dippers *Cinclus mexicanus*, Gillis et al. 2008; giant tortoises, Swingland and Lessells 1979; blackcapped tits, Perez-Tris and Telleria 2002; brown trout *Salmo trutta*,

0 Olsson and Greenberg 2004: European robins *Erithacus* 61
rubecula, Adriansen and Dhondt 1990). Nonetheless, previous studies of ungulates have suggested the potential for demographic tradeoffs between migratory and resident populations. For example, migrant moose in Scandinavia 65
5 may have benefited from reduced human hunting pressure (Andersen 1991), although possibly at the expense of lower forage quality (Andersen 1991, Ball et al. 2001). In other cases, tradeoffs in forage and predation may be determined in part by environmental variation that drives the relative demographic advantages of migration (Swingland and Lessells 1979). Nicholson et al. (1997) showed that in low precipitation years (and hence low forage), survival of migrant mule deer was lower than residents, but in normal years, migrant survival was higher. The frequency of migration in American pronghorn *Antilocapra americana* (White et al. 2007) also seemed dependent on environmental conditions, where increasing snow depth reduced migratory frequency.

Our results support maintenance of partial migration through demographic balancing of vital rates that balance population growth between migratory behaviors. Elk migratory strategies appeared relatively fixed, implying individuals adopt the migratory behavior of their mother. However, this suggests that migration would either need to be somewhat plastic, or have a genetic basis. While there may be some genetic basis for migration in other ungulates such as partially migratory woodland caribou in Alberta (McDevitt et al. 2009), the recent reintroduction of elk into Alberta following near extirpation after the turn of the century and strong genetic bottlenecks (Hicks et al. 2007) makes genetic determinism an unlikely basis for partial migration in elk. Facultative switching could occur over far longer time spans than observed in our study – a hypothesis which we are currently investigating with continued long-term monitoring. Interestingly, whether elk make true behavioral ‘choices’ to migrate or not given changing predation risk is unclear. Certainly, within summer ranges, our previous research showed individual elk vary in their propensity to select for forage or avoid predation. Whether this is related to survival is as yet unknown. Elsewhere, White et al. (2009) showed that following wolf recovery in Yellowstone National Park, elk changed distribution and migratory strategies, suggesting that the decision to migrate or not can be quite plastic. Despite some insights provided by our study and others, longitudinal studies of individuals are required to understand just how plastic migratory behavior is in ungulates.

As predicted from other ungulate migratory systems (Fryxell et al. 1988), migratory elk in our study should have had higher demographic fitness. Migrants experienced 4–5% higher forage digestibility during summer, which translated to associated with higher pregnancy rates and higher female calf weights, suggesting beneficial bottom up effects of migration (Hebblewhite et al. 2008). Despite the nutritional advantage held by migrants, the equal demographic performance of residents suggests top–down effects were paramount, negating any nutritional advantages gained by migration. Based on our previous work, we expected migrants to experience lower wolf predation risk, if only slightly (15% lower) at fine spatial scales, compared to residents (Hebblewhite and Merrill 2007). However, based on our demographic estimates here, migrants experienced higher actual predation rates for two main reasons. First, migrants experienced elevated grizzly bear predation during June migration (Hebblewhite and Merrill 2007), similar to the heightened risk experienced during migration by migratory shorebirds (Lank et al. 2003). Second, residents were able to reduce mortality by exploiting local refugia from wolves close to human activity (Hebblewhite and Merrill 2008, 2009). By remaining on low elevation winter range that provided high forage biomass during summer, but low forage quality (Hebblewhite et al. 2008), pregnancy rates and calf weights were lower for resident than migrant elk (Hebblewhite 2006, Supplementary material Appendix A2). These resident resource selection differences were mirrored by the survival models. Residents experienced the interactive effects of higher wolf predation risk and high forage biomass (lower quality in summer) through the $F \times P$ interaction in the Cox survival model (Fig. 5). As a result, resident elk should have had lower survival, but did not because they exploited human-caused refugia from predators that allowed them to select for areas of high forage biomass without the higher wolf predation risk (Hebblewhite and Merrill 2008). These results are similar to those of Frair et al. (2007) who found opposing spatial tradeoffs in mortality from humans and wolves in a study area just north of the Ya Ha Tinda population.

The larger group sizes of residents also could be an ‘extra’ advantage that helped resident fitness equal or exceed that of migrants. Because resident group sizes were 2–3 times that of migrants during summer, despite having equal population sizes, and mortality hazard declined with increasing group sizes, residents benefited from nearly a 20% mortality hazard reduction during the summer from grouping alone. The benefits of group size suggest a positive feedback mechanism when combined with predation by wolves that could cause depensatory predation above a critical elk group size-density threshold of about 75 elk (Fig. 4, sensu Fryxell et al. 2007, McLellan et al. 2010). Because residents typically occurred in a few large herds during summer, wolf encounters with residents would quickly saturate (Huggard 1993), and predation rates could become inversely density dependent as elk density, and thus herd size, increases (Hebblewhite and Pletscher 2002, McLellan et al. 2010). This suggests larger group sizes of residents may allow resident elk to ‘escape’ predation, similar to recent work on lion predation on wildebeest in the Serengeti (Fryxell et al. 2007). Critically, the development of large group sizes was only possible because of human activity which created a predation refugia on the winter range grasslands during summer (Hebblewhite and Merrill 2009), contributing to reduced mortality hazard of residents. Thus, a combination of fine-scale resource selection strategies by residents and larger group sizes allowed them to achieve similar demographic fitness as migrants.

Reconciling the equal demographic fitness between resident and migrant elk during our study with the long-term trends of declining migrants since the 1980s is a challenge, however. In the 1980s, there were approximately 30 resident elk out of 1000 elk (Morgantini 1988, Hebblewhite et al. 2006). While adult and calf survival estimates are unknown (Morgantini 1988), we know wolves were essentially absent, there was no legal female harvest, and calf:female ratios were 0.33, equivalent to a 0.40 calf survival rate (Harris et al. 2008). Therefore, we used our Leslie-matrix model to evaluate the

[AQ2]

0 effect on λ of 75% less predation mortality, no legal hunt- 61
ing, and calf survival of 0.40. Under this scenario, λ of both 62
strategies would have been 1.12 in 1980, which if constant, 63
would have resulted in 230 residents and ~2390 migrants by 64
1996, compared to a peak of 2200 elk in 1994 (Hebblewhite 65
et al. 2006). Since this peak of 2200, the M:R ratio and pop- 66
ulation size has been steadily declining to a 50:50 M:R and 67
~1000 elk. Clearly, density dependence of some form (pre- 68
dation or food competition) affected elk demography since 69
10 this peak, but differentially negatively affected migrants more 70
than residents. We think it was combined differences in wolf 71
predation and human hunting that reconciles our contrast- 72
ing short-term (this study) and long-term observations of 73
declining migrants. This is in contrast to Norwegian red 74
15 deer populations without high predation where competition 75
for food on winter ranges may actually increase migration 76
(Myrsterud et al. 2011). First, the high levels of human hunt- 77
ing residents experienced in this study did not reflect long- 78
term survival because the legal female harvest only occurred 79
20 from 1999–2003. High human-caused mortality of resi- 80
dents occurred during winter when residents and migrants 81
were mixed together on the winter range suggesting higher 82
vulnerability to hunting, perhaps through habituation to 83
human activity (Thompson and Henderson 1998) or spatial 84
partitioning (Robinson et al. 2010). Regardless, assuming 85
25 no legal hunter-caused harvest during both years (but still 86
First Nations harvest), and no changes in other vital rates, 87
resident $\lambda_R = 0.95$ and migrants $\lambda_M = 0.861$, an almost 10% 88
difference in population growth. Without any First Nation 89
harvest which occurred only in 2003, λ_R approaches 1.01. 90
30 Thus, we would expect higher survival of residents without 91
human hunting to explain the declines in the proportion of 92
migrants in this population. 93

These differences in human-caused mortality would 94
be compounded by the higher wolf mortality experienced 95
35 by migrants, which we think is the most likely density- 96
dependent mechanism explaining declines in overall popu- 97
lation size since the mid 1990s (Garrott et al. 2009). Both 98
migrant and residents were declining at 10–12% during 99
our study, largely due to high wolf predation on migrants, 100
40 and high human and wolf predation on residents. The rapid 101
decline in population size and the proportion of migrants 102
following wolf recolonization in the mid 1980's is consis- 103
tent with growing evidence suggesting wolves may be capable 104
of limiting or regulating ungulates to low densities (Messier 105
45 1994, Hebblewhite et al. 2005, Garrott et al. 2009), and 106
that wolf predation at least initially differentially impacted 107
migrants more than residents (Hebblewhite et al. 2006). 108
However, as overall elk and wolf density declines, wolf pre- 109
dation on migrants may be expected to ameliorate, providing 110
50 a density-dependent mechanism for maintenance of some low 111
frequency of migrants in the population. For example, popu- 112
lation and migrant declines have apparently stabilized since 113
2005, suggesting density-dependent declines in predation- 114
mortality (Hebblewhite unpubl.). These differences in short 115
55 and long-term dynamics emphasize the importance of long- 116
term studies to understand migratory ungulate population 117
dynamics (Bolger et al. 2008). Future population modeling 118
would help identify the ranges of predation and demographic 119
parameters under which migration will be favored in partially 120
60 migratory ungulate populations (sensu Kaitala et al. 1993). 121

Regardless of differences between long and short-term 61
observations in this population, it is clear that the demo- 62
graphic advantage of residents arose because of a complex 63
interaction between forage, predation risk, and human dis- 64
turbance. Without these interactions, forage biomass would 65
have to be much greater, or predation risk much reduced, to 66
achieve the same benefits of being resident. In the absence 67
of modern human activity on the Ya Ha Tinda winter range, 68
the demographic balance would have likely been more in 69
favor of migrants, consistent with the literature expectation 70
that migration benefits ungulates. However, many migratory 71
ungulate populations are threatened by the same suite of 72
human impacts that are leading to loss of migratory behavior 73
(Berger 2004, Bolger et al. 2008). In an adjacent elk popu- 74
lation surrounding the town of Banff, high human activity 75
in a lower habitat quality matrix for elk has also increased 76
the demographic fitness of resident elk, reducing the M:R 77
ratio to 0.15, and leading to ecosystem-scale trophic changes 78
(Hebblewhite et al. 2005, Hebblewhite 2007). Likewise, 79
in Yellowstone National Park, migrant elk are exposed not 80
only to higher predation risk from wolves and grizzly bears, 81
but also reduced forage quality on migratory summer ranges 82
because climate change has reduced the duration of access to 83
high quality forage (Middleton et al. unpubl.). While histor- 84
ically overhunting and fragmentation (roads, fences, dams) 85
seemed to be the driving forces of loss of migration in some 86
areas (Berger 2004), modern human impacts related to land- 87
use and climate change reducing benefits of migration may 88
be more important (Middleton et al. unpubl., this study). 89
For example, with climate change reductions in the growing 90
season duration (Middleton et al. unpubl.) or timing of calv- 91
ing and green up (Post et al. 2008) may differentially harm 92
migrants, migrants may be expected to be negatively affected 93
more than residents who often select for human modified 94
systems. Understanding the demography of partially migra- 95
tory ungulates will be key to anticipating and reversing losses 96
of migratory ungulates (Bolger et al. 2008). 97

In conclusion, we show that despite the benefits of higher 98
forage quality and the relatively lower wolf predation risk 99
experienced by migrants, demographic fitness of resident 100
elk remaining on the winter range was at least equal if not 101
marginally (3%) higher than residents. Differences between 102
short- and long-term dynamics helps explain the declin- 103
ing M:R ratio from 1977 of 1.5% per year obtained from 104
aerial surveys in this population. We attribute this shifting 105
balance between migrants and residents to the higher 106
human-hunting mortality experienced by residents dur- 107
ing our study, the recovery of wolves in BNP in the 1980s, 108
reduced predation on residents due to human activities in 109
summer, and the grassland habitat of the winter range that 110
facilitates large resident group sizes in summer. Although 111
our snapshot of demographic characteristics indicate simi- 112
lar population growth between the two herd segments 113
at this time, whether historic declines in the proportion 114
of migrants has stabilized is unknown, and will require 115
understanding mechanisms determining density-depend- 116
ence in survival. However, at present, despite important 117
differences in resource selection between migrant and 118
resident elk for forage and predation risk in this popu- 119
lation, both strategies seem to be achieving comparable 120
demographic fitness. 121

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