

Behavioural flexibility in migratory behaviour in a long-lived large herbivore

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Summary

1. Migratory animals are predicted to enhance lifetime fitness by obtaining higher quality forage and/or reducing predation risk compared to non-migratory conspecifics. Despite evidence for behavioural flexibility in other taxa, previous research on large mammals has often assumed that migratory behaviour is a fixed behavioural trait.

2. Migratory behaviour may be plastic for many species, although few studies have tested for individual-level flexibility using long-term monitoring of marked individuals, especially in large mammals such as ungulates.

3. We tested variability in individual migratory behaviour using a 10-year telemetry data set of 223 adult female elk (*Cervus elaphus*) in the partially migratory Ya Ha Tinda population in Alberta, Canada.

4. We used net squared displacement (NSD) to classify migratory strategy for each individual elk-year. Individuals switched between migrant and resident strategies at a mean rate of 15% per year, and migrants were more likely to switch than residents. We then tested how extrinsic (climate, elk/wolf abundance) and intrinsic (age) factors affected the probability of migrating, and, secondly, the decision to switch between migratory strategies.

5. Over 630 individual elk-years, the probability of an individual elk migrating increased following a severe winter, in years of higher wolf abundance, and with increasing age.

6. At an individual elk level, we observed 148 switching events of 430 possible transitions in elk monitored at least 2 years. We found switching was density-dependent, where migrants switched to a resident strategy at low elk abundance, but residents switched more to a migrant strategy at high elk abundance. Precipitation during the previous summer had a weak carryover effect, with migrants switching slightly more following wetter summers, whereas residents showed the opposite pattern. Older migrant elk rarely switched, whereas resident elk switched more frequently to migrate at older ages.

7. Our results show migratory behaviour in ungulates is an individually variable trait that can respond to intrinsic, environmental and density-dependent forces. Different strategies had opposing responses to density-dependent and intrinsic drivers, providing a stabilizing mechanism for the maintenance of partial migration and demographic fitness in this population.

Key-words: Banff National Park, behavioural plasticity, behavioural syndrome, *Cervus elaphus*, density dependence, elk, migration, partial migration, ungulate, Yellowstone National Park

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Introduction

Determining the causes and consequences of migratory behaviour is a unifying theme for the study of animal migration (Dingle 1996; Lundberg 2013). Partial migration, where one part of a population migrates and the other foregoes migration, is a common form of migration across diverse taxa including tropical butterflies (Sager & Malcolm 2015), fish (Brodersen *et al.* 2008), amphibians (Grayson, Bailey & Wilbur 2011) and mammals (Cagnacci *et al.* 2011). Understanding partial migration is an important ecological question: why does one strategy not dominate? There have been many eco-evolutionary models developed to explain the conditions under which partial migration can persist (Kaitala, Kaitala & Lundberg 1993; Griswold, Taylor & Norris 2011; Pulido 2011). In partially migratory populations, migration can be fixed, either through genetic or cultural inheritance, or plastic, where individuals are able to switch between strategies, with frequency- or density-dependent mechanisms regulating the proportion of migrants (Kaitala, Kaitala & Lundberg 1993; Griswold, Taylor & Norris 2011; Lundberg 2013). The theory of partial migration (Kaitala, Kaitala & Lundberg 1993) shows there must be either density-dependent demography or behavioural switching that balances the different strategies (Kaitala, Kaitala & Lundberg 1993; Lundberg 2013), or, alternately, an extrinsic threshold above which migration occurs (Pulido 2011). Despite theoretical insights, however, there have been few studies of behavioural switching across taxa (Chapman *et al.* 2011a; Festa-Bianchet 2013).

Understanding partial migration is also an important applied conservation issue because of the ecological importance and declines of migratory taxa (Bauer & Hoyer 2014), especially in large herbivores (Berger 2004; Bolger *et al.* 2008). Ungulates demonstrate some of the most dramatic, ecologically important and imperilled examples of migration (Berger 2004; Bolger *et al.* 2008). In large herbivores, migration confers demographic benefits through access to higher quality forage (Fryxell 1991) and escape from predation (Fryxell, Greever & Sinclair 1988). Yet modern human land use and exploitation have caused population declines, and shifted the demographic balance in favour of non-migrants in many populations (Berger 2004; Bolger *et al.* 2008). Bolger *et al.* (2008) argues that conservation requires an understanding of demographic and behavioural responses to environmental and human factors. In particular, understanding how behavioural flexibility can contribute to migratory persistence will be key (Berger 2004). Thus, both from a theoretical and applied viewpoint, understanding partial migration hinges on how individuals make migratory decisions.

Despite the evidence for behavioural flexibility across taxa such as amphibians (Grayson, Bailey & Wilbur 2011) and fish (Skov *et al.* 2011), in most studies of large mammals, the common assumption is that migration is a fixed trait (Fryxell, Greever & Sinclair 1988; Hebblewhite &

Merrill 2011; Middleton *et al.* 2013a). In part, this is because the long life spans of most large herbivores increase the difficulty of conducting long-term studies on marked individuals. There is also no evidence that migration is genetically determined as in some insect or avian taxa (Barnowe-Meyer *et al.* 2013; Northrup *et al.* 2014). Only recently are studies starting to highlight the behavioural flexibility of migration in large herbivores. Across a latitudinal gradient in Europe, Cagnacci *et al.* (2011) showed wide variation in the distance, timing and proportion of migratory roe deer (*Capreolus capreolus*). In Norway, Myrsetrud *et al.* (2011) showed that the proportion of migratory red deer (*Cervus elaphus*) was related to density. In Tanzania, Morrison & Bolger (2012) showed that up to 18% of individual wildebeest (*Connochaetes taurinus*) switched between wet season ranges between years, dependent on reproductive history. But a recent special forum in the journal *Ecology* (Festa-Bianchet 2013) pointed out that there have been no long-term studies in large herbivores that tested for migratory switching (Gaillard 2013), undermining our ability to understand the ecology and conservation of migration.

We tested whether migration was a fixed or behaviourally plastic trait in a partially migratory elk (*Cervus elaphus*) population using 10 years of data on 223 individual marked females from 2002 to 2012. We focus solely on females here because of their importance for polygynous ungulates (Gaillard *et al.* 2000) in driving population dynamics. We then tested how environmental and intrinsic factors affected both the probability of migrating, and the probability of switching between different migratory strategies for elk monitored over multiple years. Migrant elk in our study population were allopatric in summer, but returned to a shared winter range with residents during winter. Female migratory elk in our system experienced reduced predation risk and enhanced access to forage quality in summer (Hebblewhite & Merrill 2007; Hebblewhite, Merrill & McDermid 2008), but slightly higher predation risk during migration itself. Through fine-scale resource selection strategies (Hebblewhite & Merrill 2009), resident elk were able to nearly mitigate these differences and experienced more or less equivalent demographic fitness (Hebblewhite & Merrill 2011). Therefore, we expected migrants and resident behaviour to respond differently to environmental covariates. First, we categorized individual elk in each year as either (i) migrants with seasonal, long-distance movements between winter and summer ranges, (ii) residents that remained on their winter range in summer, or (iii) intermediate or mixed migrants that returned to a different winter range, migrated for shorter distances and or made multiple return migrations between seasonal ranges (Bunnfeld *et al.* 2011). Secondly, we then tested for how environmental and intrinsic factors affected the proportion of migrants in the population over time to assess behavioural flexibility at the population level (Myrsetrud *et al.* 2011; Singh *et al.* 2012). Thirdly, we tested whether individuals

changed strategies between years, and how extrinsic (environmental) and intrinsic factors affected the probability of switching in consecutive years. We hypothesized that the factors driving switching between strategies should differ between migrant and residents; otherwise, fixation of one strategy in the population would occur (Kaitala *et al.* 1993).

We tested several non-exclusive hypotheses (Table 1) about how environmental and intrinsic factors affected the probability of migrating and switching. The terminal investment hypothesis (Clutton-Brock 1984) predicts that as female mammals age, they should take greater risks to obtain resources for reproduction at the expense of their own survival. Therefore, we predicted that because migration provided strong nutritional benefits and reduced predation, but incurred heightened risk during migration, the probability of switching should increase with age particularly for residents. Density dependence has also been shown to affect migratory behaviour under the food competition hypothesis (Table 1), which predicts that both the proportion of migrants and probability of switching would increase at high density on shared winter range to avoid density-dependent competition during summer (Mysterud *et al.* 2011). The other forage-based hypothesis for migration, the forage maturation hypothesis, predicts that migrants will benefit from enhanced forage quality during the growing season (Hebblewhite, Merrill & McDermid 2008). Climatic variation also could be important in driving migratory behaviour. We predicted that following a severe winter that imposed high energetic costs, both the proportion of migrants and the probability of switching from a resident to a migratory strategy would increase to gain access to higher forage quality (Table 1). Similarly, because summer forage quality for ungulates is mediated by precipitation (Cook *et al.* 2004; Middleton *et al.* 2013b), we hypothesized that the year after a wet spring/summer, elk would be in better body condition with less need to migrate, and thus, we predicted a lower proportion of migrants and probability of switching from resident to migrant status. Finally, predation risk could affect migratory behaviour through den-

sity-dependent predation (Hebblewhite 2013). We predicted that at higher wolf abundance, predation risk would be higher for residents that live at lower elevations compared to migrants that move to higher elevations with lower predation risk (Hebblewhite & Merrill 2007). Thus, during years with high wolf abundance we predicted a higher probability of migrating and resident elk switching to migration. These four different hypotheses and predictions make specific predictions about both the probability of migration, frequency of switching, and direction of switching that we summarized in Table 1.

Materials and methods

STUDY AREA

The ~6000-km² study area was defined by the summer migratory movements of the Ya Ha Tinda (YHT) elk herd in and adjacent to Banff National Park (BNP; 51°30' N, 115°30' W), Alberta, Canada (Hebblewhite *et al.* 2006). This population winters on one concentrated montane rough fescue (*Festuca campestris*) winter range of 20 km² where both migrants and residents randomly mix (Fig. S2 in Appendix S2, Supporting information; Spaedtke 2009; Robinson, Hebblewhite & Merrill 2010), although migratory and resident individuals still display different antipredator behaviours in mixed groups (Robinson, Hebblewhite & Merrill 2010). We captured 323 elk, radiocollaring 223 individual females (each elk was captured an average of 1.43 times, range 1–5) from February 2002 (winter 2001/2002) to March 2011 (winter 2010/2011) using corral trapping for the majority of elk ($n = 262$ captures), supplemented by helicopter net gunning ($n = 56$) and ground darting ($n = 5$) especially to target elk whose Global Positioning System (GPS) collar blow-off devices had failed (Appendix S6; capture methods were approved under U. of Montana IACUC protocol 059-08MHCES, and Univ. of Alberta Animal Care Protocol #353112). We used 1–2 large, 0.2 ha, corral trap baited with hay in three spatial locations within 2 km from 2002 to 2012 (Fig. S3 in Appendix S2 and Fig. S6 in Appendix S6).

We captured an average of 38.1 (SD = 7.46) adult female elk/winter, deploying a mean of 6.6 GPS and 31.5 VHF collars/year. We used VHF and GPS telemetry data from February 2002 to October 2012 to test for individual behavioural flexibility

Table 1. Hypotheses and predictions about the frequency and direction of female elk (*Cervus elaphus*) switching between migratory strategies in the partially migratory Ya Ha Tinda elk population, Banff National Park, Alberta, Canada, 2002–2012

Hypothesis	Frequency of migrants	Frequency of switching	Direction of switching
Terminal investment hypothesis	More migrants at older ages	Should increase with age curvilinearly	Switch from resident to migrant
Forage maturation hypothesis	More migrants following severe winters, dry summers	Should increase following severe winters and/or dry summers	Switch to migrant following severe winters and/or dry summers
Competition avoidance hypothesis	More migrants at higher elk density	Should increase at higher elk abundance	Switch to migrant at higher elk density to avoid food competition
Numeric response hypothesis (density-dependent predation hypothesis)	More migrants at higher wolf density	Should increase at higher wolf abundance	Switch to migrant at high wolf abundance because of higher predation risk on residents

in migration. GPS collars collected one location every 2 h (minimum), and we obtained VHF locations every 6–9 days for a total of ≥ 10 locations per season (winter, summer) per individual. We frequently recaptured individuals, replacing GPS collars with VHF collars to extend the period of monitoring of switching rates, critical for this study, after GPS collars had expired (typically 2 years with this fix rate schedule). We estimated age for a subset of elk ($n = 81$) by cementum annuli ageing of the vestigial canine in live elk or incisors from elk mortalities (Hamlin *et al.* 2000).

ENVIRONMENTAL COVARIATES

Elk population size was surveyed every winter when migrants and resident animals were sympatric on shared winter range using aerial helicopter surveys with an average sightability adjustment (Hebblewhite 2000). Population size declined during our study from ~ 1200 in 2002 to ~ 500 in 2014 after stabilizing in 2010 (Fig. S4 in Appendix S2). We obtained weather data from a nearby Environment Canada weather station (Dogrib station, Hebblewhite *et al.* 2006). We derived an index of winter severity by taking the absolute value of the product of winter (November–March) temperature (Celsius) by the winter precipitation (cm) such that cold and snowy winters would be high severity and high values. Similarly, we derived an index of spring and summer precipitation as the total precipitation (cm) from May to September. Hebblewhite & Merrill (2011) showed that wolf predation was the most important cause of mortality for adult female elk and that the most important predictor of predation risk was the numeric response (both spatial and temporal, Hebblewhite & Merrill 2007). Therefore, we developed an annual index of predation risk using wolf abundance for this study. We estimated wolf abundance using a census of the number and size of wolf packs occurring in the study area by summing late winter pack sizes within the study area. For each pack, we determined the maximum number of individuals observed in February and March from direct observations, annual snow-tracking surveys (Hebblewhite 2006), and a network of over 50 remote cameras. We expected elk spring migration strategies to be driven by the preceding winter's wolf numbers.

CLASSIFYING MIGRATORY BEHAVIOUR

We used a combination of net-squared displacement (NSD; Bunnefeld *et al.* 2011) estimated from VHF and GPS telemetry and *ad hoc* spatial rules (*sensu* Mysterud *et al.* 2011) to classify individual migratory behaviour in each year (see Eggeman 2012 for more details). NSD measures the cumulative squared displacement from an arbitrary starting point (defined here as 1 April, see below). We then fit NSD for each individual elk in each year to one of five movement models as defined by Bunnefeld *et al.* (2011): migrant, mixed migrant, resident, nomads and dispersers in linear and nonlinear mixed-effects models. We selected the best movement model for each individual elk-year using AIC_c and AIC_c weights (Eggeman 2012). We censored individual VHF radiocollared elk with insufficient locations (< 20) and resampled GPS data to one location per day at random with first location date on or after 1 April. We considered additional spatial constraints to help discriminate migratory strategies: migrants needed to have non-overlapping seasonal ranges for a minimum period of 30 days, residents needed to remain within 15 km of the win-

ter range during summer based on winter home range radii, and individuals that moved > 15 km from their winter range for < 30 days were mixed migrants. With this combination of NSD and spatial rules, we classified all elk as either (i) migrant, (ii) resident or (iii) mixed migrant.

SWITCHING BETWEEN MIGRATORY STRATEGIES

Next, we estimated switching rates between migrant, mixed/intermediate migrant and resident strategies for those elk that were monitored for ≥ 2 consecutive years. We then grouped mixed/intermediate migrants with migrants because both migrated away from a winter range to a distant summer range, but mixed migrants were allowed to return to a slightly different winter range than their starting location (Mysterud *et al.* 2011). We then tested whether individual elk switched from one strategy to another strategy in the following year. We estimated the switching rate to be the number of all collared elk monitored ≥ 2 years that switched between 2 years (year t to $t + 1$) as a proportion of the number of elk that we monitored in both years. We also estimated the switching rates of intermediate migrants to either migrant or resident behaviour.

PROBABILITY OF MIGRATING AND SWITCHING

First, we tested the probability that an individual migrated (combining migrant and mixed migrants) in any elk-year as a function of intrinsic and extrinsic covariates. Secondly, we tested whether the probability an individual elk switched strategies from 1 year to the next was affected by these same covariates, and whether the effect of covariates differed between strategies. Age was the only intrinsic covariate, and extrinsic covariates were total spring/summer precipitation (cm, May–September), winter severity index, wolf abundance and elk abundance; all extrinsic covariates were linked to the preceding winter or summer (in the case of precipitation). We used generalized linear (Binomial) mixed-models (Zuur *et al.* 2009) to model the probability of migration, $P(\text{Migrant})$, and the probability of switching strategies, $P(\text{Switch})$, accounting for repeated measures using a random intercept for each individual elk (Gillies *et al.* 2006). All covariates were standardized to optimize estimation (Zuur *et al.* 2009). We included all monitored individuals in the $P(\text{Migrant})$ model, but only those individuals monitored for ≥ 2 years to detect switching between strategies in the $P(\text{Switch})$ model. Furthermore, because we had known age for only a subset of all individual elk, we first built models of $P(\text{Migrant})$ and $P(\text{Switch})$ without age, and then, considered a second set of models including age as a covariate using the reduced data set. We also considered all plausible two-way interactions. For the $P(\text{Switch})$ model, we included interactions with migratory status to test whether different strategies responded differently to environmental and intrinsic covariates. For each analysis, we constructed an all-inclusive candidate set of models, and then used AIC_c (Burnham & Anderson 1998) to select the top model(s). We screened for collinearity between covariates using a conservative threshold of $r = 0.3$ to guard against confounding (Zuur *et al.* 2009). We also tested for potential confounding differences in age between migratory strategies. Because the proportion of migrants may have been an artefact of capture methods (Fieberg & Conn 2014), we examined the effects of capture methods, capture location, whether individuals were recaptured, and capture event on the probability of migration, but found no effects of any capture variable on P

(Migration) (Appendix S6). Finally, we assessed model fit using the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow 2000), as well as using the receiver operating curves (ROC) to estimate AUC as a measure of predictive performance (Hosmer & Lemeshow 2000). All analyses were conducted in R (R Core Team 2014) using the packages LME4, NLME, AICCMODAVG, GGPlot2 and ROCR (Pinheiro & Bates 2000; Sing *et al.* 2005; Wickham 2009; Bates *et al.* 2014; Mazerolle 2015).

Results

Of our sample of 223 adult female elk over the 10-year study period, we observed 107 mortalities (Eggeman 2012) and censored a total of 17 elk-years because of insufficient relocation data. We monitored 630 elk-years of migratory status to estimate the $P(\text{Migrant})$ model. We monitored 148 individual elk at least 2 or more years (mean of 3.7 years for consecutively monitored elk, range 2–8 years) for a total of 420 potential switching events. Ages of 81 known-age elk averaged 7.17 (SD = 3.77) ranging from 0 to 22 years, and these 81 known-age elk were observed over 136 potential switching events. There were no differences in mean ages of elk between migratory strategies (ANOVA $F_{2,81} = 2.41$, $P = 0.14$), nor elk that switched between strategies (ANOVA $F_{2,81} = 1.14$, $P < 0.4$), and no trend in mean age of elk in different migratory strategies over the study (linear regression $P = 0.34$ for migrants, $P = 0.22$ for residents). There was little collinearity between our environmental or intrinsic covariates; all pairwise correlations were $r \leq 0.30$ and few were statistically significant. The exceptions were the expected (Hebblewhite & Merrill 2009) positive correlation between wolf and elk abundance ($r = 0.75$, $P = 0.0001$), and wolf abundance and spring/summer precipitation ($r = 0.76$, $P < 0.000001$). Therefore, in development of our candidate model set, we did not enter these two pairs of covariates together in the same model. As expected, mean elk age weakly increased with elk abundance ($r = 0.225$,

$P = 0.001$) given that our population declined (Fig. S4 in Appendix S2); however, importantly, we did not detect any correlation of age with any other covariates.

CLASSIFYING MIGRATORY BEHAVIOUR

We classified a mean of 36% ($n = 24.3$, SE = 3.03) of the elk as migrants, 10% ($n = 6.4$, SE = 0.95) as intermediate migrants, 53% ($n = 35.6$, SE = 3.38) as residents and 1% ($n = 0.6$, SE = 0.22) dispersers (Table 2, see Appendix S1 for migratory statistics and Fig. S3 in Appendix S2 for example classification of NSD curves). The percentage of individuals classified as migrants varied over time but not in any clear direction (Table 2). The proportion of individuals migrating showed no relationship with density ($r = 0.33$, $P = 0.41$) nor time ($r = -0.40$, $P = 0.24$, Table 2). While dispersal events were rare (1% of switches), only migrants dispersed, although this was not statistically significant because of the low frequency of dispersal (Table 2). There were no differences between migratory statistics (dates, distances, etc.) between migrant or mixed-migrant strategies (Eggeman 2012), nor trends over time in such statistics, with one exception. We found a positive relationship with yearly mean distance of migration and the proportion of marked elk that were migratory ($r^2 = 0.70$, $P = 0.009$).

PROBABILITY OF MIGRATION

The top-ranked model explaining whether an individual elk migrated was a function of wolf abundance and winter severity preceding the spring migration (Table 3; Table S5 in Appendix S5 for AIC table). The model fit well, failing to reject the Hosmer–Lemeshow goodness-of-fit test ($\chi^2 = 3.799$, d.f. = 8, $P = 0.11$), but showed weak predictive performance with an AUC score of 0.64. The second-ranked model had a $\Delta\text{AICc} = 1.49$, an Akaike weight of 0.25, and contained a significant effect of wolf, a weaker

Table 2. Percentage of female elk (*Cervus elaphus*) classified into different migratory strategies (migrant, mixed migrant/intermediate, resident and disperser) using the Bunnefeld *et al.* (2011) method in the Ya Ha Tinda elk population, Banff National Park, Alberta, Canada, 2002–2012. Year is migration year from 1 April to 31 March of the following year, and the correlation ($\text{cor}(x, t)$), and associated P -value, between annual proportions in each migratory category (x) and time (t) is shown for each strategy

Year	Migrant (n)	Mixed/Intermediate (n)	Resident (n)	Disperser (n)
2002/2003	52.6% (20)	13.2% (5)	31.6% (12)	2.6% (1)
2003/2004	43.0% (34)	12.7% (10)	44.3% (35)	0.0% (0)
2004/2005	46.5% (40)	8.1% (7)	43.0% (37)	2.3% (2)
2005/2006	38.4% (28)	4.1% (3)	57.5% (42)	0.0% (0)
2006/2007	30.3% (20)	12.1% (8)	56.1% (37)	1.5% (1)
2007/2008	33.3% (19)	5.3% (3)	59.6% (34)	1.8% (1)
2008/2009	15.8% (9)	8.8% (5)	75.4% (43)	0.0% (0)
2009/2010	24.3% (18)	5.4% (4)	68.9% (51)	1.4% (1)
2010/2011	27.8% (20)	16.7% (12)	55.6% (40)	0.0% (0)
2011/2012	52.2% (35)	10.4% (7)	37.3% (25)	0.0% (0)
Total	36% (233)	10% (64)	53% (356)	1% (6)
$\text{cor}(x, t)$, P	$r = -0.43$, $P = 0.23$	$r = -0.02$, $P = 0.91$	$r = 0.41$, $P = 0.23$	$r = -0.50$, $P = 0.31$

winter severity effect, and a non-significant interaction between wolf*winter. Likewise, the third-ranked model ($\Delta\text{AIC} = 2.54$, Akaike weight = 0.15) was solely a function of wolf abundance. Elk and spring/summer precipitation occurred only in much lower ranking models (Appendix S5). Therefore, we chose to focus solely on reporting the top model of wolf and winter severity. The probability of an elk migrating increased following severe winters and at higher wolf density (Table 3, Fig. 1a,b).

Considering the subset of data with known age, the leading $P(\text{Migrant})$ model fit the data moderately well (Hosmer–Lemeshow goodness-of-fit test, $\chi^2 = 15.80$, d.f. = 8, $P = 0.055$) with higher, but still only moderate predictive capacity ($\text{AUC} = 0.699$). The top model was a function of elk age + wolf abundance, with 0.56 of the Akaike weight (Appendix S5; the second-ranked model was age + wolf abundance + winter, $\Delta\text{AIC} = 1.47$, Akaike weight = 0.27), and the third- and last-ranked model in the top model set was age + wolf + winter + wolf \times winter ($\Delta\text{AIC} = 2.81$, Akaike weight = 0.14, Table S5 in Appendix S5). Despite the fact that the 95% confidence interval of the β coefficient for winter severity overlapped zero in the second-ranked model, we report this model in Table 4 to facilitate comparison to the full model without age, which otherwise had the same structure. In the age model, the probability of migration also increased following severe winters (although the 95% confidence interval overlapped zero), with higher wolf abundance, but also in older aged individuals (Fig 3c).

SWITCHING BETWEEN MIGRANT AND RESIDENT STRATEGIES

We found evidence for switching between migratory strategies among elk that we monitored ≥ 2 years (Table 4). Of 420 potential switching events across all elk-years, we observed 148 switching events. Mean annual switching rate between migrant and resident strategies

remained relatively constant regressed against time ($r = 0.01$, $P = 0.73$) with a range between 10% and 23% (mean = 16%, $\text{SE} = 1.39$, Table 4, Fig. 2). Migrants tended to switch more than residents (Fig. 2, Table 4), with 52% of all migrants switching compared to 32% of residents (Fig. 2, $\chi^2 = 13.7$, d.f. = 3, $P\text{-value} = 0.0015$). Figure 3 shows one individual elk monitored for ≥ 2 years who switched from a resident to migratory behaviour in 2003 and 2004, as evidenced with the NSD nonlinear models. Some animals switched almost every year, but many never switched (Fig. 2). The overall switching rate was unrelated with elk abundance (linear regression, $\beta = -0.006$, $r^2 = 0.15$, $P = 0.28$, Table 2), but switching rates of migrants versus residents differed. When we compared switching rates of migrant, intermediate migrant or resident strategies, the proportion of elk that switched between intermediate migratory behaviours and all other behaviours was 10% higher than for elk in other strategies (χ^2 test = 18.59, $P < 0.0001$), ranging from 13% and 32% (mean = 22%, $\text{SE} = 0.02$, $n = 9$). Nonetheless, for subsequent analyses of switching, we considered only migrants and resident behaviours.

There were two close models for consideration that best explained the probability of switching (Table S5 in Appendix S5 for AIC tables). The top model (AICc weight = 0.4) described switching as a function of elk abundance and its interaction with migratory status, as well as spring/summer precipitation and its migratory interaction. The second-ranked model ($\Delta\text{AICc} = 0.15$, AICc weight = 0.37) was a function of elk abundance and migratory status. Winter had only weak support in the top model set (Table S5 in Appendix S5), and there was no support for wolf abundance affecting switching; thus, we report only the top model here. The top $P(\text{Switch})$ model fit the data reasonably well (H–L gof test, $\chi^2 = 6.799$, d.f. = 8, $P = 0.07$), and had strong predictive capacity with a $\text{AUC} = 0.842$. The probability of switching with increasing elk abundance declined for a migrant, but increased for a resident (Fig. 4a, Table 5); that is,

Table 3. Top logistic regression models for the probability of an individual elk migrating [$P(\text{Migrant})$, where 1 = migrant strategy, including migrant and mixed-migrant strategies, 0 = resident] as a function of standardized covariates and random effect of elk (1|elk_id) without (left) and with (right) age included as a covariate, Ya Ha Tinda elk population, 2002–2012, Alberta, Canada. We present the second-ranked age model here to facilitate comparison between models (see Table S3 in Appendix S5 for model selection tables)

Model	$P(\text{Migrant}) \sim \beta X + (1 \text{elk_id})$			$P(\text{Migrant}) \sim \text{Age} + \beta X + (1 \text{elk_id})$		
AICc weight	0.54, first-ranked model			0.27, second-ranked model		
Sample size	$N = 630$ elk-years, $n = 206$ unique elk			$N = 190$ elk-years, $n = 64$ unique elk		
(1 elk_id)	Variance (1 elk) = 10.58, SD = 3.253			Variance (elk) = 9.35, SD = 2.993		
Standardized covariate	Estimate	SE	Pr(> z)	Estimate	SE	Pr(> z)
Intercept	−0.322	0.297	0.279	−0.191	0.787	–
Wolf abundance	0.683	0.180	<0.00005	1.599	0.592	0.0055
Winter severity	0.305	0.144	0.0349	0.258	0.225	0.2530
Age	–	–	–	1.754	0.775	0.0173

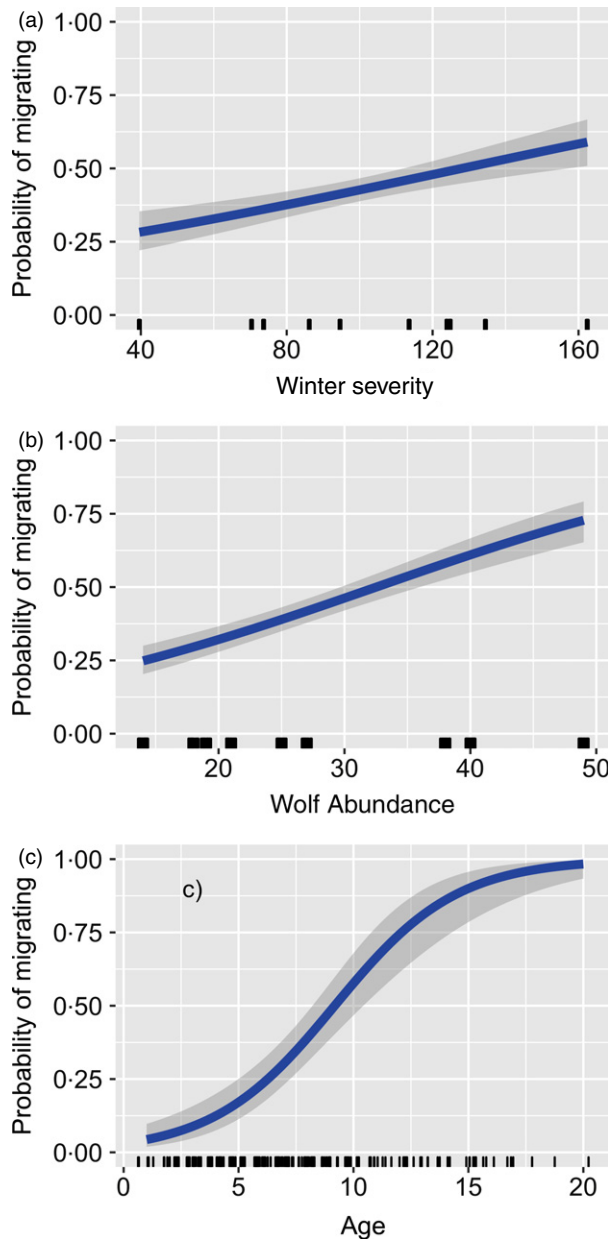


Fig. 1. Probability of a female elk (*Cervus elaphus*) migrating from the winter range to summer range at time t as a function of (a) winter severity in the winter immediately preceding migration ($t - 1$), (b) wolf abundance in the previous winter ($t - 1$) and (c) individual age at t (as estimated from cementum annuli) for elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002–2012.

more animals switched from resident to migrant at higher elk abundance, and vice versa at lower elk abundance. The probability a resident switched strategies was unaffected by previous spring/summer precipitation (Fig. 4b, Table 5), but migrants did switch slightly more to be a migrant after a dry previous summer.

Finally, when we considered only the known-age individuals with the potential to switch strategies, the best model had the majority of the Akaike weight (0.54, second-ranked model was 0.11), so we focus only on this model. Considering age, switching was a function of age

and elk abundance with differences in the effect of elk abundance and age on switching between migratory strategies (Table S6 in Appendix S5, Table 5). This model had reasonable fit (H–L gof test, $\chi^2 = 3.799$, d.f. = 8, $P = 0.11$), and it had the highest predictive capacity with an AUC = 0.91. Despite small sample sizes, controlling for the effects of elk age increased the strength of the interactive effects of elk density by migratory strategy, although the 95% CIs overlapped (Table 4). Similar to the full model without age, migrants switched more to resident at low elk abundance, and vice versa. The probability of switching as a function of age contrasted between resident and migrant elk; migrants tended to stop switching as they aged, whereas residents showed some tendency to increase switching (Fig. 4c).

Discussion

By following individual elk over a 10-year period, our results demonstrate that migratory behaviour is a flexible behavioural trait, capable of dynamically responding to both intrinsic and environmental covariates. Flexibility in migratory behaviour has been previously demonstrated in many other taxa; Grayson, Bailey & Wilbur (2011) showed red-spotted newts (*Notophthalmus viridescens*), switched between resident and migratory strategies in a conditional dependent fashion; Skov *et al.* (2011) showed bream (*Abramis brama*), a freshwater fish, altered their migratory strategy based on predation risk; and in many bird populations, migration is body size dependent/age dependent (Lack 1968; Adriaensen & Dhondt 1990). Most previous research on large herbivores, however, including our own, assumed migration to be fixed (Middleton *et al.* 2013a,b), or only addressed variation in migration between populations (Cagnacci *et al.* 2011; Myrsterud *et al.* 2011; Singh *et al.* 2012). Our study provides multiple lines of evidence for behavioural flexibility in migratory behaviour in large herbivores at the individual level (Tables 2 and 4). The probability of migrating varied in response to both intrinsic (age) and environmental covariates that demonstrated migratory flexibility at the population level over time. At the individual level, our results demonstrate behavioural switching between strategies, where some individual elk switched between strategies as much as every other year (Fig. 2), while others never switched. Moreover, there were different drivers of switching between strategies dependent on the starting migratory state, highlighting the conditional, facultative nature of migration in ungulates. Although few other studies tracked individual behaviour over multiple years, in one example, White *et al.* (2014) tracked 67 moose (*Alces alces*) over an average of 3 years found that 21% of individuals switched between migratory strategies at least once. In a 2-year study of impala (*Aepyceros melampus*) in Zimbabwe, Gaidet & Lecomte (2013) showed that 12% of residents in year 1 switched to a migratory strategy in year 2 whereas 10% of migrants switched to a resident

Table 4. Number of female elk (*Cervus elaphus*) that switched between migratory strategies [migrant = migrants and mixed migrants (M), residents (R), dispersers (D), defined according to the Bunnefeld *et al.* (2011) approach, see text] that were monitored for two consecutive years or more in the Ya Ha Tinda elk population, Banff National Park, Alberta, Canada, 2002–2011. The number monitored, number and percentage of monitored elk that switched/year, and the proportion (Pr) of those that switched among migration strategies are shown

	No.	No. switching/year	Pr. switching	R → M	Pr.	M → R	Pr	M → D	Pr
2002–2003	34	5	0.15	0	0	5	1	0	0
2003–2004	56	8	0.14	3	0.38	4	0.5	1	0.125
2004–2005	59	9	0.15	0	0	9	1	0	0
2005–2006	53	11	0.21	7	0.64	4	0.36	0	0
2006–2007	41	6	0.15	4	0.67	1	0.17	1	0.16
2007–2008	40	4	0.10	0	0	4	1	0	0
2008–2009	46	5	0.11	2	0.4	2	0.4	1	0.2
2009–2010	65	15	0.23	13	0.87	2	0.13	0	0
2010–2011	56	9	0.16	8	0.89	1	0.11	0	0
Mean	50	8	0.16	4.1	0.32	3	0.52	1	0.06
SD	10.3	3.5	0.04	4.5	0.36	2.4	0.38	0	0.09
SE	3.4	1.17	0.01	1.5	0.12	0.8	0.13	0	0.03
Total	450	72	0.16	37		30		3	

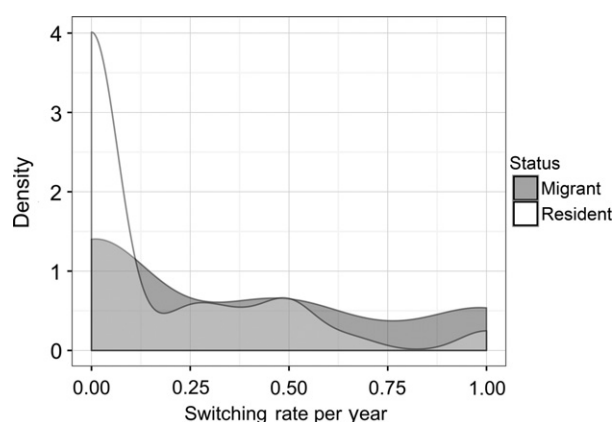


Fig. 2. Migratory flexibility in a partially migratory elk population in Ya Ha Tinda, Banff National Park, Alberta, Canada, 2002–2011, showing the kernel density distribution of individuals switching between strategies per year (# switches by an elk/# years monitored) by the migratory strategy in the preceding year.

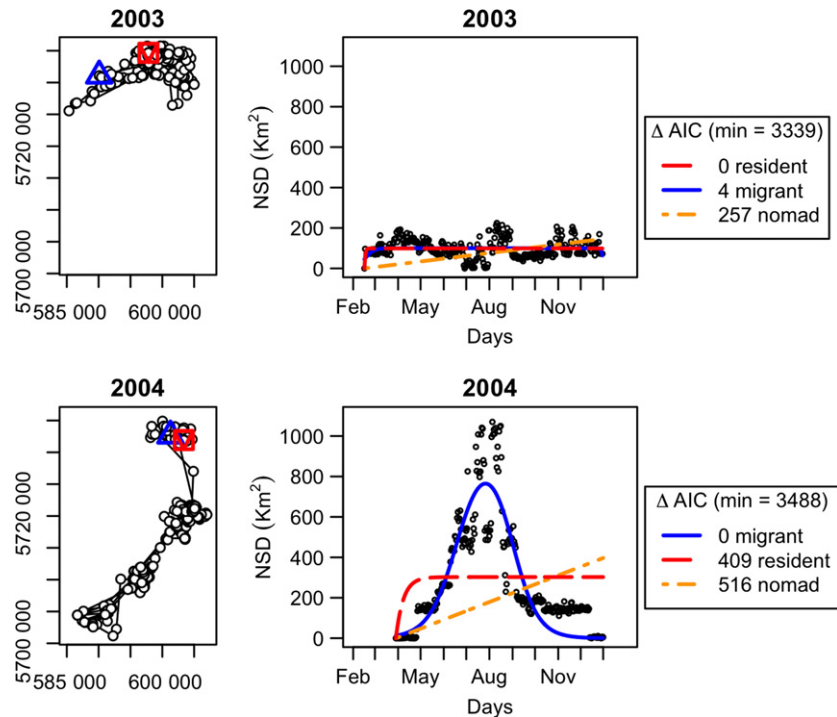
strategy. Nelson (1998) clearly showed that migratory behaviour can change from that learned from one's mother in white-tailed deer (*Odocoileus virginianus*) by following marked mother–daughter pairs over multiple years. Combined with no evidence for genetic determinism for migratory behaviour in ungulates (Barnowe-Meyer *et al.* 2013; Northrup *et al.* 2014), our results and work on other taxa suggest that the null hypothesis should be that ungulates can, and do, switch between migratory strategies.

In one of the only other studies examining switching over time in elk, Cole *et al.* (2015) found little evidence for switching between migratory strategies for 129 elk monitored >2 years in the Jackson Hole elk herd. One obstacle in comparing our results to theirs is that Cole

et al. (2015) used a different approach to classify migratory behaviour in their system, and there were no clear residents. Thus, methodological differences in the classification of migration may still be obscuring switching between strategies. Despite the challenges of the 'Bunnefeld' method in classifying migratory behaviour, standardizing classification has been a big advance in the field of migration to facilitate between study comparisons (Cagnacci *et al.* 2016). Regardless of the potential methodological difference, there may also be context dependence affecting behavioural flexibility in migration. Perhaps flexibility in migratory behaviour will not be adaptive in some populations. Nonetheless, other studies in Jackson Hole demonstrate migratory flexibility in elk. For example, Jones *et al.* (2014) showed that supplemental feeding reduced the duration migratory elk spent on summer range, delayed their migration, and caused other migratory changes reflecting behavioural flexibility. So while elk may not have been switching *per se* between strategies in Jackson Hole, notwithstanding the different definitions of migration, they were clearly demonstrating plasticity in migratory behaviour consistent with sensitivity to bottom-up, forage drivers.

Switching between migratory strategies may accommodate shifting trade-offs between risk and forage to maximize lifetime reproductive success across spatiotemporal scales. Consistent with both the food competition and predation hypotheses, the probability of migrating was higher at higher wolf and elk abundance, which would both help elk avoid competition on shared winter range during summer with residents, and escape predation by dispersing across the landscape. We also found a strong positive relationship with yearly mean distance of migration and the percentage of migratory elk ($r^2 = 0.70$, $P = 0.009$), suggesting distance was related to the frequency of migrant elk, also supporting both the predation

Fig. 3. Switching between migratory strategies for an individual female elk (*Cervus elaphus*; elk #93) revealed through nonlinear modelling of net-squared displacement (NSD) following Bunnefeld *et al.* (2011). The top row shows elk #93 in 2003 as resident elk with movements within a typical 10-km² home range (geographic space in top left with coordinates in metres; starting and ending location shown by a red triangle and blue square, respectively) and NSD versus time shown in top right, with model selection for the migrant (including mixed migrant), resident and nomadic movement models. The bottom row shows elk #93 in 2004 when she migrated 25 linear km from the winter range clearly fitting a migrant strategy.



and competition hypotheses (Table 1). These results are consistent with Myrsetrud *et al.* (2011) who showed that red deer migration increased at higher densities, as well as their migratory distance. Yet in their study in Norway, predation by non-human predators was unimportant, and few other studies have tried to understand effects of predation on migratory behaviour. In our study, predation by grey wolves was the leading cause of mortality on adult female elk and the likely cause of the steady population decline from ~1200 to 500 during our study (Hebblewhite & Merrill 2011; Eggeman 2012). At high elk population size, predation may have been concentrated on the largest group sizes of resident elk, which occurred on the winter range year round (Hebblewhite & Pletscher 2002). As elk densities, and wolf abundance and predation risk, declines, predation risk on residents and migrants may equilibrate, or even heighten on migrants because of the greater group sizes of resident elk during summer that would dilute individual predation risk (Hebblewhite & Merrill 2011). Thus, declining predation risk could lead to changes in switching.

Whereas the overall probability of switching did not change as the elk population (and wolf) declined, the direction of switching did and the overall probability of migrating decreased. This is more consistent with the view that predation risk, and not the benefits of forage, changed at low elk (and wolf) abundance. Although wolf abundance out-competed elk abundance from a model selection perspective, the collinearity we found between wolf and elk abundance makes clear interpretation of density-dependent effects, whether from predation, or forage, challenging. At high elk and wolf abundance, migrant elk tended to stay migrants, reducing their switching rates,

whereas resident elk tended to migrate more. As both elk and wolf densities declined, the probability of migration declined, and more individuals switched to resident behaviour. More studies are needed to disentangle top-down and bottom-up influences. Regardless, the countervailing responses of migrant and resident elk across elk densities support predictions of the theory of partial migration (Kaitala *et al.* 1993). Opposing density-dependent switching rates would tend to stabilize partial migration, leading to a long-term average proportion of migrants in the population (Grayson, Bailey and Wilbur 2011).

We also found migratory behaviour was sensitive to environmental variation consistent with bottom-up, forage-based hypotheses similar to other studies (Cagnacci *et al.* 2011; Myrsetrud *et al.* 2011; Singh *et al.* 2012; Jones *et al.* 2014). Red deer across Norway were more likely to migrate in areas of mountainous topography, consistent with obtaining high-quality forage (Myrsetrud *et al.* 2011). Elk in Jackson Hole, WY, reduced the duration and distance they migrated to obtain higher quality forage if they received supplemental winter food on feedgrounds (Jones *et al.* 2014). Roe deer increased the probability of migration with increasing snow depth in a site (Cagnacci *et al.* 2011). In contrast, between-population analysis of moose migration by Singh *et al.* (2012) showed that increasing snow depth decreased the probability of migration within a population, but only in areas with high road density. In our study, given migration improved access to high forage quality (Hebblewhite, Merrill & McDermid 2008), we expected that the proportion of migrants and the degree of switching would favour migration following severe winters and dry summers, which our results only weakly confirmed. After dry summers, residents switched to

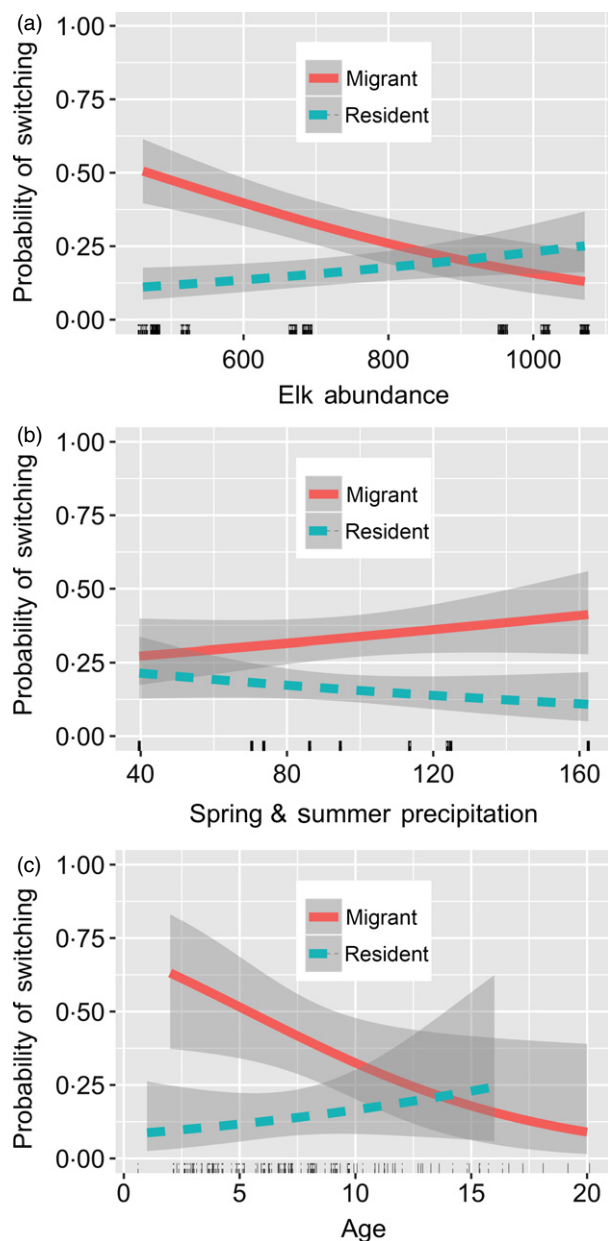


Fig. 4. Probability of individual female elk switching between migratory strategies from year $t - 1$ to t as a function (a) elk abundance in the previous winter ($t - 1$), and (b) spring and summer precipitation in the preceding summer, $t - 1$, and (c) individual age (as estimated from cementum annuli) at t for migrant (red) and resident (blue) elk in the Ya Ha Tinda elk population, Alberta, Canada, 2002–2012.

migratory behaviour 25% of the time, but after a wet previous summer, switched to a migratory behaviour only 10% of the time (Fig 4b). At the same time, migrants were relatively indifferent to environmental variation in switching between strategies, presumably because they already obtained high-quality forage.

In large herbivores, age effects likely manifest at the life-history strategy level like litter size (Hamel *et al.* 2009) and investment in male vs. female offspring in polygynous breeders (Clutton-Brock 1984). In the only

study on age effects on large herbivore migration, moose demonstrated reduced migratory tendency with senescence (Singh *et al.* 2012), contrary to the predictions of the terminal investment hypothesis if migration is predicted to increase access to forage and reduce predation (Table 1). Perhaps moose migration in Sweden may arise because of other factors. Consistent with these predictions, in our population, elk migrated more as they aged, taking more risks from predation by wolves but also grizzly bears especially during the brief, but risky, migratory phase itself (Hebblewhite & Merrill 2007) to obtain the bottom-up benefits of forage. Resident elk, in contrast, tended to stay residents while young, perhaps trading-off short-term survival versus long-term reproductive fitness by selecting human-induced refugia from predation (Hebblewhite & Merrill 2009), but then switched to a migratory strategy as they aged: migrants rarely switched after ageing (Fig. 4c). The effects of age will likely vary across species and populations dependent on the risk-forage trade-off (Hamel *et al.* 2009; Nilsen *et al.* 2009).

Despite evidence for density dependence in switching rates, previous studies showed almost no demographic differences between migratory strategies in this population (Hebblewhite & Merrill 2011; Eggeman 2012). At first this seemed like a confusing result – why were we not seeing differences between migrants and residents? Other studies in other taxa similarly have reported equivalent fitness pay-offs between migrant and residents, for example, in American dippers (*Cinclus mexicanus*, Gillis *et al.* 2008). We hypothesize that migrants and residents may switch between strategies in response to perceived intrinsic fitness of that strategy, but because of density-dependent habitat selection, they may achieve equivalent realized fitness pay-offs (Haugen *et al.* 2006). Indeed, the magnitude of the switching rates between strategies (~15%/year) may actually be the reason for few demographic differences between strategies. This is an important, but subtle point: migration itself may be in response to anticipated demographic fitness outcomes, not a consequence, through an ideal free distribution (Haugen *et al.* 2006). Indeed, our statistical power to detect switching between strategies was low until close to 10 years of monitoring (M. Hebblewhite, unpublished data). Previous estimates of annual switching rates for ungulates at 2% per year from this population (Hebblewhite & Merrill 2011), ~6% for moose (White *et al.* 2014), ~10% for impala (Gaidet & Lecomte 2013), and 0.2% from short-distant to long-distant migrant elk (Cole *et al.* 2015) almost certainly underestimate true switching rates. Therefore, population modelling for partially migratory ungulates may need to account for switching between strategies.

We also found preliminary evidence for a correlation between behavioural traits in migratory flexibility. Migrants tended to have higher switching rates, and only migrant animals dispersed, though our sample sizes for dispersers were small. This is suggestive that migratory

Table 5. Top logistic regression model(s) for the probability of elk switching (1 = switch, 0 = did not switch) between migratory strategies as a function of standardized covariates, Ya Ha Tinda elk population, 2002–2012, Alberta, Canada, with individual elk (elk_id) as a random effect, without (left) and with (right) age included as a covariate (see Table S3 in Appendix S5 for model selection tables)

Model	$P(\text{Switch}) \sim \text{BX} + (1 \text{elk_id})$			$P(\text{Switch}) \sim \text{Age} + \text{BX} + (1 \text{elk_id})$		
AICc weight	0.40, first-ranked model			0.54, first-ranked model		
Sample size	$N = 418$ elk-years, $n = 148$ individual elk			$N = 136$ elk-years, $n = 55$ unique elk		
(1 elk_id)	Variance (elk) = 12.08, SD = 3.476			Variance (elk) = 7.273, SD = 2.675		
Standardized covariate	Estimate	SE	Pr(> z)	Estimate	SE	Pr(> z)
Intercept	−7.16	1.302	<0.00005	−6.05	2.323	0.0092
Migrant	10.92	2.430	<0.00005	10.17	4.010	0.0112
Elk N	0.787	0.280	0.0048	1.500	0.757	0.0480
Elk $N \times$ Migrant	−3.797	0.841	<0.00005	−4.337	2.068	0.0360
Spring precip	0.346	0.221	0.117	—	—	—
S_precip \times Migrant	−1.476	0.735	0.044	—	—	—
Age	—	—	—	−0.155	0.749	0.41
Migrant \times Age	—	—	—	−0.157	0.113	0.09

See Supporting information for full model selection results.

behaviour may be a behavioural syndrome in ungulates, as in other taxa (Nilsson 2010; Chapman *et al.* 2011b). Long-term studies in roe deer showed bold animals were more likely to disperse and that 'boldness' was strongly positively correlated with other behavioural measures, including habitat selection (Debeffe *et al.* 2014; Bonnot *et al.* 2015). Further work is needed to test whether migration is a behavioural syndrome, and what the consequences are for conservation.

One of the important limitations of our study is the lack of information about individual reproductive status. In other taxa, reproductive status is a strong determinant of subsequent migratory strategy (Grayson, Bailey & Wilbur 2011). Morrison & Bolger's (2012) study showed that wildebeest in Tanzania switched summer/wet season ranges more following successful reproduction, but White *et al.* (2014) showed that previous reproductive history did not affect whether moose switched migratory strategies. We know that in northern temperate ungulates, because of the high costs of lactation during summer, female ungulates that successfully raise a juvenile through winter will be in worse body condition than females who either do not breed (alternate year reproduction) or lose their offspring early (Cook *et al.* 2013; Middleton *et al.* 2013b). Thus, we expect that the year after successfully rearing a juvenile to recruitment (1-year old), females would tend to migrate more where there are greater benefits from forage for migrants, relative to predation risk. Future studies should collect individual reproductive success to be able to test this hypothesis. Nevertheless, our study clearly demonstrates, that, like many other vertebrate taxa (Chapman *et al.* 2011a; Grayson, Bailey & Wilbur 2011; Nilsson *et al.* 2014), migratory behaviour in large herbivores varied at the population and individual level consistent with age, density, predation risk and envi-

ronmental covariates. Long-term monitoring of individually marked migratory individuals is the only clear way to test the ultimate drivers and consequences of migratory behaviour (Gaillard 2013).

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Data accessibility

Global Positioning System (GPS) and VHF telemetry data are available on the MOVEBANK data repository (associated with Movebank project ID 72264071; data repository doi: 10.5441/001/1.k8s2g5v7, Hebblewhite & Merrill 2016).

References

- Adriaansen, F. & Dhondt, A.A. (1990) Population-dynamics and partial migration of the European robin (*Erythacus rubecula*) in different habitats. *Journal of Animal Ecology*, **59**, 1077–1090.
- Barnowe-Meyer, K.K., White, P.J., Waits, L.P. & Byers, J.A. (2013) Social and genetic structure associated with migration in pronghorn. *Biological Conservation*, **168**, 108–115.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.
- Bauer, S. & Hoyer, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, **344**, 1242552.
- Berger, J. (2004) The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, **18**, 320–331.

- Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**, 63–77.
- Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B. *et al.* (2015) Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, **26**, 105–114.
- Brodersen, J., Nilsson, P.A., Hansson, L.A., Skov, C. & Bronmark, C. (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, **89**, 1195–1200.
- Bunnfeld, N., Boerger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. *et al.* (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, **80**, 466–476.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY, USA.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N. *et al.* (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, **120**, 1790–1802.
- Cagnacci, F., Focardi, S., Ghisla, A., Van Moorter, B., Gurarie, E., Heurich, M. *et al.* (2016) How many routes lead to migration? Re-establishing the link between definitions, methods and movement ecology. *Journal of Animal Ecology*, **85**, 54–68.
- Chapman, B.B., Bronmark, C., Nilsson, J.A. & Hansson, L.A. (2011a) The ecology and evolution of partial migration. *Oikos*, **120**, 1764–1775.
- Chapman, B.B., Hultén, K., Blomqvist, D.R., Hansson, L.A., Nilsson, J.A., Brodersen, J. *et al.* (2011b) To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, **14**, 871–876.
- Clutton-Brock, T. (1984) Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. *et al.* (2004) Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.
- Cook, R.C., Cook, J.G., Vales, D.J., Johnson, B.K., McCorquodale, S.M., Shipley, L.A. *et al.* (2013) Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs*, **184**, 1–45.
- Cole, E.K., Foley, A.M., Warren, J.M., Smith, B.L., Dewey, S.R., Brimyer, D.G. *et al.* (2015) Changing migratory patterns in the Jackson elk herd. *The Journal of Wildlife Management*, **79**, 877–886.
- Debeffe, L., Morellet, N., Bonnot, N., Gaillard, J.M., Cargnelutti, B., Verheyden-Tixier, H. *et al.* (2014) The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. *Proceedings of the Royal Society B-Biological Sciences*, **281**, 1790.
- Dingle, H. (1996) *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford, UK.
- Egge-man, S. (2012) *Migratory Behavior and Survival of Adult Female Elk in a Partially Migratory Population*. Master of Science, University of Montana, Missoula, MT, USA.
- Festa-Bianchet, M. (2013) Forum: human-induced reversal of fortunes for migratory ungulates? *Ecology*, **94**, 1245–1256.
- Fieberg, J.R. & Conn, P.B. (2014) A hidden Markov model to identify and adjust for selection bias: an example involving mixed migration strategies. *Ecology and Evolution*, **4**, 1903–1912.
- Fryxell, J.M. (1991) Forage quality and aggregation by large herbivores. *The American Naturalist*, **138**, 478–498.
- Fryxell, J.M., Greever, J. & Sinclair, A.R.E. (1988) Why are migratory ungulates so abundant? *The American Naturalist*, **131**, 781–798.
- Gaidet, N. & Lecomte, P. (2013) Benefits of migration in a partially-migratory tropical ungulate. *BMC Ecology*, **13**, 36.
- Gaillard, J.M. (2013) Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. *Ecology*, **94**, 1261–1264.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gillies, C., Hebblewhite, M., Nielsen, S.E., Krawchuk, M., Aldridge, C., Frair, J. *et al.* (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.
- Gillis, E.A., Green, D.J., Middleton, H.A. & Morrissey, C.A. (2008) Life history correlates of alternative migratory strategies in American dipers. *Ecology*, **89**, 1687–1695.
- Grayson, K.L., Bailey, L.L. & Wilbur, H.M. (2011) Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology*, **92**, 1236–1246.
- Griswold, C.K., Taylor, C.M. & Norris, D.R. (2011) The equilibrium population size of a partially migratory population and its response to environmental change. *Oikos*, **120**, 1847–1859.
- Hamel, S., Gaillard, J.M., Festa-Bianchet, M. & Cote, S.D. (2009) Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, **90**, 1981–1995.
- Hamlin, K.L., Pac, D.F., Sime, C.A., DeSimone, R.M. & Dusek, G.L. (2000) Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *Journal of Wildlife Management*, **64**, 441–449.
- Haugen, T.O., Winfield, I.J., Vollestad, L.A., Fletcher, J.M., James, J.B. & Stenseth, N.C. (2006) The ideal free pike: 50 years of fitness-maximizing dispersal in Windermere. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2917–2924.
- Hebblewhite, M. (2000) *Wolf and Elk Predator–Prey Dynamics in Banff National Park*. Wildlife Biology Program, School of Forestry, University of Montana, Missoula, MT, USA.
- Hebblewhite, M. (2006) *Linking Predation Risk and Forage to Ungulate Population Dynamics*. University of Alberta, Edmonton, Alberta, Canada.
- Hebblewhite, M. (2013) Consequences of ratio-dependent wolf predation on elk population dynamics. *Population Ecology*, **55**, 511–522.
- Hebblewhite, M. & Pletscher, D.H. (2002) Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, **80**, 800–809.
- Hebblewhite, M. & Merrill, E.H. (2016) Data from: Behavioral flexibility in migratory behavior in a long-lived large herbivore. *Movebank Data Repository*, doi:10.5441/001/1.k8s2g5v7.
- Hebblewhite, M. & Merrill, E.H. (2007) Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia*, **152**, 377–387.
- Hebblewhite, M. & Merrill, E.H. (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, **90**, 3445–3454.
- Hebblewhite, M. & Merrill, E.H. (2011) Fitness balancing in a partially migratory ungulate through risk–forage trade-offs. *Oikos*, **120**, 1860–1870.
- Hebblewhite, M., Merrill, E.H. & McDermid, G. (2008) A multi-scale test of the forage maturation hypothesis for a partially migratory montane elk population. *Ecological Monographs*, **78**, 141–166.
- Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E. *et al.* (2006) Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. *Wildlife Society Bulletin*, **34**, 1280–1295.
- Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*. John Wiley and Sons, New York, NY, USA.
- Jones, J.D., Kauffman, M.J., Montieth, K.L., Scurlock, B.M., Albeke, S.E. & Cross, P.C. (2014) Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications*, **24**, 1769–1779.
- Kaitala, A., Kaitala, V. & Lundberg, P. (1993) A theory of partial migration. *American Naturalist*, **142**, 59–81.
- Lack, D. (1968) Bird migration and natural selection. *Oikos*, **19**, 1–9.
- Lundberg, P. (2013) On the evolutionary stability of partial migration. *Journal of Theoretical Biology*, **321**, 36–39.
- Mazerolle, M.J. (2015) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3.
- Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A. *et al.* (2013a) Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, **94**, 1245–1256.
- Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Jimenez, M.D., Cook, R.C., Cook, J.G. *et al.* (2013b) Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters*, **16**, 1023–1030.
- Morrison, T.A. & Bolger, D.T. (2012) Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*, **81**, 543–552.
- Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V. & Meisingset, E. (2011) Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos*, **120**, 1817–1825.
- Nelson, M.E. (1998) Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology*, **76**, 426–432.
- Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., van Laere, G. *et al.* (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, **78**, 585–594.

- Nilsson, A.L.K. (2010) Migratory and resident blue tits *Cyanistes caeruleus* differ in their reaction to a novel object. *Naturwissenschaften*, **9**, 981–985.
- Nilsson, J.A., Bronmark, C., Hansson, L.A. & Chapman, B.B. (2014) Individuality in movement: the role of animal personality. *Animal Movement Across Scales* (eds L.A. Hansson & S. Akesson), pp. 90–109. Oxford University Press, Oxford, UK.
- Northrup, J.M., Shafer, A.B.A., Anderson, C.R., Coltman, D.W. & Wittemyer, G. (2014) Fine-scale genetic correlates to condition and migration in a wild cervid. *Evolutionary Applications*, **7**, 937–948.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-Plus*. Springer-Verlag, New York, NY, USA.
- Pulido, F. (2011) Evolutionary genetics of partial migration – the threshold model of migration revisited. *Oikos*, **120**, 1776–1783.
- R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robinson, B.W., Hebblewhite, M. & Merrill, E.H. (2010) Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia*, **164**, 265–275.
- Sager, B.H. & Malcolm, S.B. (2015) Evidence for partial migration in the Southern Monarch Butterfly, *Danaus erippus*, in Bolivia and Argentina. *Biotropica*, **35**, 1–8.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2005) ROCr: visualizing classifier performance in R. *Bioinformatics*, **21**, 7881.
- Singh, N.J., Boerger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, **22**, 2007–2020.
- Skov, C., Baktoft, H., Brodersen, J., Bronmark, C., Chapman, B., Hansson, L.A. *et al.* (2011) Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1414–1418.
- Spaadtke, H.R. (2009) *Aversive Conditioning on Horseback: A Management Alternative for Grassland Systems Threatened by Sedentary Elk Populations*. Master of Science, University of Alberta, Edmonton, Alberta, Canada.
- Wickham, H. (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York, NY, USA.
- White, K.S., Barten, N.L., Crouse, S. & Crouse, J. (2014) Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology*, **95**, 225–237.
- Zuur, A.E., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed-Effects Models and Extensions in Ecology in R*. Springer, New York, NY, USA.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Summary migration statistics for the partially migratory Ya Ha Tinda elk herd.

Appendix S2. Supplementary figures of the study area, migratory classification using NSD, and sightability adjusted-population trends over time.

Appendix S3. Scatterplot matrix of environmental covariates used in *P*(Migrant) and *P*(Switching) analyses.

Appendix S4. Proportions of migrant and resident elk by categories of environmental and intrinsic covariates.

Appendix S5. Model selection tables for the probability of migrating with and without age as a covariate, and for the probability of switching again without and with age as a covariate.

Appendix S6. Description of capture methods and assessment of the effects of capture methods on the probability of migration.