# ARTICLE



# Large herbivores in a partially migratory population search for the ideal free home

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# Abstract

Migration is a tactic used across taxa to access resources in temporally heterogenous landscapes. Populations that migrate can attain higher abundances because such movements allow access to higher quality resources, or reduction in predation risk resulting in increased fitness. However, most migratory species occur in partially migratory populations, a mix of migratory and nonmigratory individuals. It is thought that the portion of migrants in a partial migration population is maintained either through (1) a population-level evolutionary stable state where counteracting density-dependent vital rates act on migrants and residents to balance fitness or (2) conditional migration, where the propensity to migrate is influenced by the individual's state. However, in many respects, migration is also a form of habitat selection and the proportion of migrants and residents may be the result of density-dependent habitat selection. Here, we test whether the theory of Ideal Free Distribution (IFD) can explain the coexistence of different migratory tactics in a partially migratory population. IFD predicts individuals exhibit density-dependent vital rates and select different migratory tactics to maximize individual fitness resulting in equal fitness ( $\lambda$ ) between tactics. We tested the predictions of IFD in a partially migratory elk population that declined by 70% with 19 years of demographic data and migratory tactic switching rates from >300 individuals. We found evidence of density dependence for resident pregnancy and adult female survival providing a fitness incentive to switch tactics. Despite differences in vital rates between migratory tactics, mean  $\lambda$  (fitness) was equal. However, as predicted by the IFD, individuals switched tactics toward those of higher fitness. Our analysis reveals that partial migration may be driven by tactic selection that follows the ideal free distribution. These findings reinforce that migration across taxa may be a polymorphic behavior in large herbivores where migratory tactic selection is determined by differential costs and benefits, mediated by density dependence.

#### **KEYWORDS**

behavioral polymorphism, Cervus canadensis, ideal free distribution, migratory switching, partial migration

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# INTRODUCTION

Migration is a tactic used across taxa to access resources in temporally heterogeneous landscapes (Dingle, 2014). For many species, this seasonal movement also reduces exposure to predation risk (Fryxell et al., 1988; Hebblewhite & Merrill, 2007; McKinnon et al., 2010). Migration is ecologically important because it allows species to reach higher abundances than possible if they remained as residents (Fryxell & Sinclair, 1988). Across taxa, migratory populations and historic migratory routes have declined and even disappeared worldwide (Berger, 2004; Harris et al., 2009; Wilcove & Wikelski, 2008), further increasing the importance of knowing how migration is maintained and the consequences of its loss.

Most migratory species exhibit partial migration, where a proportion of the population seasonally migrates and the rest remain as residents year-round (Chapman et al., 2011). This generates the intriguing ecological questions of why some individuals do not migrate, or why all do not adopt one tactic or the other. Partial migration is a classic behavioral polymorphism (Chapman et al., 2011) thought to be maintained in a population through two mechanisms. First, partial migration could be maintained as a population-level evolutionary stable state, where the proportion of migrants is dictated by counteracting density-dependent survival and/or reproduction of migrants and residents that provide the mechanism to balance fitness (Cressman & Křivan, 2006; Kaitala et al., 1993; Lundberg, 1987). For example, the ratio of migrants and residents in partially migratory populations of obligate migrants such as mule deer (Odocoileus hemionus) that display high fidelity to specific migratory tactics or routes, would be governed by the density-dependent vital rates experienced by each tactic. However, for species with migratory flexibility, the tactic specific density-dependent factors alone may not explain migrant to resident ratios. A second mechanism is conditional migration where an individual's propensity to migrate is influenced by their state, for example, where migration is dependent on reproductive state (Brodersen et al., 2008; Chapman et al., 2011; Swingland & Lessells, 1979). Such conditional migration requires a mechanism, such as physiological requirements, or competitive exclusion, that influences the ability of an individual to choose a migratory tactic. For example, where fitness benefits of migration is limited by intraspecific competition, partial migration can be thought of as a form of density-dependent habitat selection writ large (Gaudry et al., 2015). Thus, partial migration can be viewed within the framework of Ideal Free Distribution (Cressman & Křivan, 2006; Fretwell & Lucas, 1970; Haugen et al., 2006; Morris, 2006).

The theory of Ideal Free Distribution (IFD) predicts that when animals have ideal information about the quality of a habitat and they have the freedom to access the habitat, then individuals will distribute themselves among habitat patches of different quality in a densitydependent manner resulting in equal mean individual fitness among individuals using different habitat patches (Fretwell & Lucas, 1970; Holt, 2001). In the case of partial migration, a habitat patch can be represented by the migratory tactic choice of seasonal range with individuals having knowledge of the fitness consequences of their tactic choice and the ability to switch between migratory tactics. Thus, if tactic-specific population growth  $(\lambda, \text{ lambda})$  was density dependent, IFD would predict equal fitness for migrant and resident individuals even if allopatric ranges vary in quality. This might seem counterintuitive if migration is thought to have evolved to benefit migrants, for example, in the classic case where migrant wildebeest (Connochaetes taurinus) of Serengeti have been found to vastly outperform residents (Fryxell et al., 1988; Hopcraft et al., 2015). Nevertheless, there are a growing number of studies demonstrating equivalent fitness between migrant and resident strategies (Gillis et al., 2008; Hebblewhite et al., 2018). A recent metaanalysis of 18 species across taxa showed equal fitness between migratory tactics (Buchan et al., 2020), with often opposing differences among vital rates for migratory tactics. For example, in mammals, reproduction was higher in migrants whereas survival was higher in residents. This is consistent with counteracting density dependence operating on migrants and residents (Buchan et al., 2020; Kaitala et al., 1993).

A key requirement of the IFD is that individuals are free to select the habitat patch or migratory tactic that maximizes individual fitness, contrary to ideal despotic distribution where sociality and territoriality prevent individuals from freely choosing habitat patches or tactics (Fretwell & Lucas, 1970). Despite previous studies that implicitly assumed large herbivores were fixed in their choice of migratory tactic, recent studies show substantial behavioral flexibility in the year-to-year decision to migrate (Eggeman et al., 2016; reviewed in Berg, 2019). Only recently have studies tested for and found evidence for migratory switching in most (Berg et al., 2019; Cagnacci et al., 2011; Gaillard, 2013; Morrison & Bolger, 2012; Mysterud et al., 2011), but not all (Sawyer et al., 2019), large herbivores. This suggests individuals are aware of the fitness consequences of migratory decisions and can choose tactics that maximize fitness or switch from a tactic if fitness is low. Unfortunately, despite Bolger et al.'s (2008) decade-old plea, few studies have tested whether individual switching between migratory tactics is the mechanism stabilizing partially

migratory populations, because such studies require long-term monitoring (Bolger et al., 2008; Gaillard, 2013).

Here we test whether individual elk in a partial migratory population follow predictions of the IFD as applied to migrant and resident tactics. We assess the IFD in a longterm study of elk (Cervus canadensis) using 19 years of individual demography data in the Ya Ha Tinda population in Banff National Park, Alberta. If individual elk in a partially migratory population follow the IFD, then we make three predictions based on Fretwell and Lucas (1970). First, we predict that there will be density dependence in vital rates, resulting in density-dependent tactic selection. For example, one tactic may experience higher vital rates across all densities, or switch tactics at an intermediate density because of differential density dependence. Second, we predict that individuals select the tactic with higher fitness. This prediction is consistent with individuals having ideal knowledge of the fitness consequences and the ability to select other migratory tactics. Similar to what Haugen et al. (2006) found in a natural experimental test of IFD in pike (Esox lucius), once fitness is equalized between tactics through density-dependent tactic selection, we predict there would be a net switching rate (i.e., tactic selection) toward the tactic of higher density-independent fitness as individuals are attempting to maximize individual fitness. Third, we expect that the fitness (as measured by tactic-specific population growth rate, lambda,  $\lambda$ , (McGraw & Caswell, 1996) of the different migratory tactics (migrants, residents) will be equal (Fretwell & Lucas, 1970). Following McGraw and Caswell (1996), we define annual fitness as the annual contribution to average fitness of a migratory tactic quantified by population growth rate, lambda, and define average tactic fitness as the geometric mean population growth rate, lambda, across years within a migratory tactic.

# MATERIAL AND METHODS

# **Data collection**

We analyzed 19 years of demographic and migratory data from the Ya Ha Tinda elk population in and adjacent to Banff National Park (BNP), Alberta, Canada. Since 2001, we tracked demography of migratory and resident individual elk using radiotelemetry, monitoring pregnancy, survival, and recruitment. The population declined from ~1600 in 2001 to around 500 elk since 2010, providing an ideal setting to test predictions of density-dependent habitat selection. The leading cause of predation is by gray wolves (*Canis lupus*), followed by hunting by humans and grizzly bears (*Ursus arctos*) (Hebblewhite et al., 2018). For more details on the study area see Hebblewhite et al. (2006).

Like most temperate ungulates, elk in our system migrate in summer. The summer (May-September) range consists of three distinct areas used by different migratory tactics: (1) residents that remain on or adjacent to the winter range rough fescue (Festuca campestris) grassland year-round, (2) eastern migrants that migrate eastward to low elevation foothills where timber harvest and oil and gas extraction generates early seral foraging opportunities, and (3) western migrants that migrate into highquality forage in high-elevation summer ranges in BNP (Figure 1). Each summer range has different levels of forage quality and predation risk by human and non-human predators (Hebblewhite & Merrill, 2009), but the shared winter range (October-April) is a low-elevation, snowfree montane grassland. Because of the low densities on our summer ranges, and thus weaker expected strength of density dependence (e.g., Mysterud et al., 2011), here, we focus on testing effects of density dependence on the shared winter range on choice of migratory tactics.

Theory shows density dependence on sympatric seasonal ranges, and not allopatric ranges, drives partially migratory population dynamics (Kaitala et al., 1993). High densities on our shared elk winter range are expected to have stronger negative impacts on year-round residents, because migrants move to lower density, higher forage quality summer ranges (Hebblewhite et al., 2008). The winter range (resident summer range) in our study system is a rough fescue grassland grazed by both residents and migrants in winter and spring. Previous studies have suggested that the lower quality resident summer range results in resident females coming into winter in poorer condition than migrants (Hebblewhite et al., 2008). Thus, bottom-up drivers of density dependence during winter would have a stronger effect on residents than migrants. Furthermore, density-dependent constraints on winter forage of residents are supported by resident females being more likely to switch tactics the year following a summer of low precipitation (Eggeman et al., 2016).

We developed an integrated population model (IPM, sensu Besbeas et al., 2002, Kéry & Schaub, 2011) to test the three predictions of the IFD using 19 years of movement and demographic data from 341 elk. The IPM model allowed us to test the effect of winter range density on the vital rates, switching rates, and lambda, which we define as expected individual fitness (McGraw & Caswell, 1996), for each of the three migratory tactics.

# Integrated population model and parameterization

IPM models use a combination of population-level data with varying levels of certainty and quality to estimate



**FIGURE 1** Ya Ha Tinda study site in Banff National Park (BNP, green), and surrounding provincial lands in Alberta, Canada showing 95% isopleths of kernel density of eastern (gray), resident (yellow), and western (blue) elk between the average end of spring migration (June 23) and the average end of fall migration (October 10), 2002–2019. Note that, because individual timing of migration varies, both the western range and eastern 95% isopleths overlap with the resident range

population growth ( $\lambda$ ) and demographic rates (Besbeas et al., 2002; Johnson et al., 2010; Kéry & Schaub, 2011). IPMs consist of biological process and observation models that are linked, allowing the variances between respective data sources to be integrated into the population estimates. We parameterized the IPM from estimates of survival, fecundity, calf: adult ratios, and population abundance using a two-stage approach. First, we analyzed the input data sets independently to produce annual demographic estimates and associated error in model inputs. Second, we created an observation model within the IPM that drew from distributions of vital rate estimates and errors from step 1 (Besbeas et al., 2002; Moeller et al., 2021). The two-stage approach allows for better mixing of MCMC chains and faster convergence of the model.

Model inputs consisted of annual estimates of adult elk survival, migratory switching rates, and pregnancy rates from marked individuals, annual counts of elk and calf: cow ratios on winter ranges based on ground and aerial surveys, and 9 years of calf survival estimates from mark-resight of known-tactic adult females (Hebblewhite et al., 2018; Hebblewhite & Merrill, 2011). We fit the IPM to data from each of the three migratory tactics separately but allowed individuals to switch tactics at the beginning of each biological year (June 2) based on yearly estimated switching rates (sensu Eggeman et al., 2016). Changes in number of individuals in each tactic were due to reproduction, mortality, and individuals changing migratory tactics; however, the population estimates of the tactics were constrained by estimates of total population size counted on the winter range. When calculating tactic-specific  $\lambda$ , we accounted for individuals changing migratory tactics at t + 1 so  $\lambda$  was a measure of fitness (reproduction and mortality) and the change in population size at t + 1 was not a result of tactic switching. We used the vital rates estimated within the model to test for the differential effects of density dependence on vital rates among the migratory tactics. We estimated the geometric mean of lambda across years to estimate the mean fitness of each tactic (McGraw & Caswell, 1996). Lambda was calculated by dividing the

number of individuals within each migratory tactic (m) at the end of the year  $N_{m,t}$  by the number of individuals at the beginning of the year  $N_{Junem,t-1}$  (see Equation 1). Thus, lambda did not include changes due to switching. This step was essential to distinguish the fitness contribution of each tactic to the overall population.

We used a sex-specific, stage-structured, post- birth pulse, matrix model with the biological year beginning on June 2 and ending on June 1 (i.e., biological year 2018 spans 2 June 2018–1 June 2019). On the model anniversary at the end of the biological year in year *t*, individuals fell into the following age classes: calves (1 year), year-lings (2 years), and adult (3+ years). Thus, the reported population sizes of each migratory tactic on June 1 represent the number of individuals that were in the tactic in year *t* – 1 after switching occurred (Equation 1) and then underwent the tactic specific process model (Equation 2):

$$N_{\text{June }m,t,a,s} = N_{m,t,a,s} \times \psi_{\text{res}-m,t} + N_{\text{west},t,a,s} \times \psi_{\text{west}-m,t} + N_{\text{east},t,a,s} \times \psi_{\text{east}-m,t}$$
(1)

 $N_{June}$  is the number of animals in migratory tactic *m* at time *t* of age *a* and sex *s*, and  $\psi$  is the switching rate from the migratory tactics of resident (res), western (west), and eastern (east) to migratory tactic *m*. The process model of each tactic is described by a 3 × 3 matrix (Caswell, 2001):

$$\begin{bmatrix} N_{m,\text{Calf},s} \\ N_{m,\text{Yrl},s} \\ N_{m,\text{A},s} \end{bmatrix}_{t} = \begin{bmatrix} 0 & 0 & \rho_{m,\text{A}} \times \phi_{m,\text{Calf}} \times 0.5 \\ \phi_{m,\text{Yrl},s} & 0 & 0 \\ 0 & \phi_{m,\text{A},s} & \phi_{m,\text{A},s} \end{bmatrix}_{t-1} \\ \times \begin{bmatrix} N_{\text{June},m,\text{Calf},s} \\ N_{\text{June},m,\text{Yrl},s} \\ N_{\text{June},m,\text{A},s} \end{bmatrix}_{t-1}$$
(2)

The matrix describes the expected number of elk in each tactic (in Equation 2) at time t based on the age-specific vector of abundances at time June t - 1 and the vital rates in in year t - 1. The number of elk at time t is a function of the following tactic specific vital rate parameters: fecundity  $\rho$ , survival  $\phi$ , and the sex ratio of calves (assumed to be 0.5) and the age-specific vector of abun- $(N_{\text{Junet-1}})$  after tactic switching occurred dance (Equation 1). We set both yearling and calf fecundity to zero because most elk do not reproduce at that age (Toweill & Thomas, 1982) and Raithel et al. (2007) found yearling fecundity had the lowest deterministic elasticity effect on population growth rate and in life-stage simulation analysis yearling fecundity explained close to 0% of the variation in lambda. We used the matrix model in Equation 2 to estimate the expected population sizes in year t as a deterministic function of the vital rates and

population size in t - 1. However, we accounted for demographic stochasticity within the *biological process model* by defining the true population size as a probability distribution centered around the expected population size at time *t* (Schaub & Abadi, 2011).

We used a normal approximation of the binomial distribution to model the number of calves and adults in a tactic in year t as a function of the number of individuals in that tactic on 1 June (Equation 1) and survival. The normal approximation allowed for better MCMC chain mixing and faster run times (Brooks et al., 2004). The number of adults  $N_A$  in year t of sex s was modeled as:

$$N_{m,t,A,s} \sim \text{Normal}(N_{\text{June }m,t,A,s} \phi_{m,t-1,A,s}, \tau)$$
 (3)

$$\tau_{m,t\,\mathrm{A},s} = \left| \left( N_{\mathrm{June}\ m,t,\mathrm{A},s} + 1 \right) \phi_{m,t,\mathrm{A},s} \left( 1 - \phi_{m,t-1,\mathrm{A},s} \right) \right|^{-1} \quad (4)$$

Where the number of adults  $N_A$  in tactic *m* of sex s on the model anniversary in year *t* is a function of the animals  $N_{June}$  that switched into the tactic after the previous model anniversary on June 1 (Equation 1) and survived at rate  $\phi$  in the previous year t - 1. Yearling abundance in year t was modeled in a similar way by using the calf abundance at t - 1 and yearling survival in t - 1. Within the IPM, we set yearling male and female survival to be equal to adult female survival for each tactic because other studies have found that there is no significant difference between yearling and adult female survival (Keller et al. 2015; Raithel et al., 2007).

We estimated the number of elk calves  $N_{m,t,\text{Calf},s}$  produced in each tactic *m* from the number of adult female elk in that tactic after switching  $N_{m,t,A,f}$ , the average pregnancy rate  $\rho_{m,t-1}$  of the tactic, and calf survival  $\phi_{m,t-1,\text{Calf}}$ . We used the normal approximation of the Poisson distribution for the number of calves (Eacker et al., 2017) in migratory tactic *m* of sex *s* in year *t* and assumed an equal sex ratio in the population (Berg, 2019)

$$N_{m,t,\text{Calf},s} \sim \text{Normal}\left(\frac{1}{2}N_{m,t,\text{A},F} \times \rho_{m,t-1} \times \phi_{m,t-1,\text{Calf}}, \tau\right)$$
(5)

$$\tau_{m,t,\text{Calf},s} = \left| \frac{1}{2} N_{m,t,\text{A},F} \times \rho_{m,t-1} \times \phi_{m,t-1,\text{Calf}} \right|^{-1}.$$
 (6)

### Data used as model inputs

We collected data on the biological parameters of survival  $\phi$ , pregnancy  $\rho$ , abundance *N*, and migratory switching  $\psi$  for each of the age classes and sexes included in the

model (see Eggeman et al., 2016; Hebblewhite et al., 2018 for full details). The data collection process and estimation of the data used to inform the biological process model briefly included (1) minimum counts from winter aerial surveys (Hebblewhite et al., 2006), (2) calf: adult age ratios from ground observations in January-April (Harris et al., 2008), (3) Kaplan-Meier survival estimates of radiocollared adults (Hebblewhite et al., 2018), (4) fecundity (pregnancy) estimates from captured females (Noyes et al., 1997), (5) Cormack-Jolly-Seber estimates of calf survival from cow-calf resight (Bonenfant et al., 2005; Lukacs et al., 2004), (6) and tactic switching rates from radiocollared individuals (Eggeman et al., 2016). Male switching rates were assumed to be equal to female switching rates because we only monitored males in the last year of the study. We observed no difference in male survival (Martin, 2021a) between tactics so this should not affect winter range population estimates.

To estimate the demographic parameters in the biological process model, we built observation process models within the IPM to account for the variance of the data sources (see Appendix S1 for a detailed description of the observation models). We modeled age ratios  $y_r$ , pregnancy rates  $y_{\rho}$ , and survival outside  $y_{\phi}$  of the IPM in step 1 of the two-stage approach to fitting the IPM and used the estimate and standard errors from these models to inform observation models used to estimate the biological process parameters. We used minimum counts from aerial surveys to inform the lower bounds of abundance estimates in the model. We classified migratory behavior using the MigrateR package in program R (R Core Team, 2020), which uses net squared displacement and a nonlinear modeling approach (Bunnefeld et al., 2011) to classify radiocollared individual migratory behavior (Eggeman et al., 2016). Switching rates were estimated from individuals collared for >1 year following Eggeman et al. (2016) independent of the IPM. We applied these switching rates directly to the individuals in each tactic (Equation 1).

# **MODEL ESTIMATION**

We solved the joint likelihood of the observation model using JAGS version 4.2.0 (Plummer, 2003) and R version 4.0.0 (R Core Team, 2020). We ran three chains for 100,000 iterations thinning every third iteration after 50,000 iterations of burn-in. We used semi-informative priors ( $\sigma = 0.2$ ) to utilize previous knowledge. We defined the priors using a Normal distribution with mean adult female survival 0.90, adult male survival 0.80, calf survival 0.30, and pregnancy rates 0.80 based on this and other elk populations (Barber-Meyer et al., 2008; Eacker et al., 2016; Raithel et al., 2007). We included a fixed effect of migratory tactics for overall differences, and a random effect of year by migratory tactic allowed for calf survival, adult survival, and pregnancy to vary over time. We allowed year-to year variability in parameters because of the variability in pregnancy rates and calf survival observed in other studies. We visually inspected trace plots and posterior densities to assess model and parameter convergence and used Brooks-Gelman-Rubin statistic to assess MCMC chain convergence (Brooks & Gelman, 1998).

To test our density-dependent predictions, we used generalized-linear models (GLM) with a Gaussian link to test the effect of standardized population size on the vital rates from the IPM. We used the point estimates for yearly vital rate from the IPM and fit these abundance BLM's models outside of the IPM framework. We included a fixed effect of migratory tactic and an interaction between population size on the winter-range and migratory tactic to determine if population-size effects on the vital rates among migratory tactics differed.

# RESULTS

We found evidence in support of our first prediction of the IFD, that vital rates were density dependent, providing a mechanism for density-dependent habitat selection. We found a negative effect of density on adult survival rates in the resident tactic ( $\beta = -0.004$ , SE = 0.001, p = 0.013), but not for other migratory tactics' survival (Figure 2a). Pregnancy rates also were weakly negatively density dependent, but also only for residents ( $\beta = -0.060$ , SE = 0.009, p < 0.001) (Figure 2b). There was no effect of winter-range population size on the young-of-year survival for any tactic (p > 0.1; Figure 2c).

We also found evidence for the second prediction of the IFD that elk switched toward the migratory tactic with higher fitness. The probability of switching between two tactics was positively related to the differential fitness of the tactics in the previous year with individuals switching toward the tactic of higher fitness ( $\beta = 0.284$ , SE = 0.108, p < 0.01, Figure 3). Specifically, the mean annual switching rate was highest for elk switching from the western migratory tactic (x = 0.199, 95% CRI = 0.083–0.341) to the resident tactic, whereas switching rates from eastern migrant to the resident tactic (x = 0.084, 95% CRI = 0–0.995) and resident to the eastern migrant tactic (x = 0.077, 95% CRI = 0.029– 0.149) did not differ. There was evidence for positive density-dependence in switching from the eastern tactic



**FIGURE 2** Switching and point estimates of vital rates estimated in the IPM of the eastern (gray), resident (yellow), and western (blue) migratory tactics as a function of female winter range density indicates density dependent switching, resident pregnancy rates, and resident calf survival

to being a resident, although weaker than overall switching rates ( $\beta = 0.049$ , SE = 0.015, p < 0.01; Figure 2d).

The mean lambda was <1 for all tactics (Figure 4), corresponding to the observed population decline (Figure 5), although abundance stabilized later in the study. Nevertheless, we found evidence for our third prediction of the IFD that there was equivalent fitness among migratory tactics. Despite the slightly higher fitness in the resident tactic ( $\lambda = 0.953$ , 95% CRI = 0.855– 1.08) than both eastern ( $\lambda = 0.904$ , 95% CRI = 0.706– 1.25) and western ( $\lambda = 0.904$ , 95% CRI = 0.771–1.1) tactics, there was no significant difference between the median fitness of the tactics (Figure 5). The higher resident elk fitness was driven by higher adult female survival (x = 0.931, 95% CRI = 0.829–0.981) compared to the eastern (x = 0.843, 95% CRI = 0.793–0.891) or western tactics (x = 0.850, 95% CRI = 0.814–0.884). However, higher pregnancy rates and calf survival of both eastern and western migrants equalized fitness among tactics (Figure 3). Pregnancy rates were lowest in the resident tactic (x = 0.847, 95% CRI = 0.731–0.956), followed by the western tactic (x = 0.909, 95% CRI = 0.859-0.958), and highest in the eastern tactic (x = 0.957 95% CRI = 0.909-1). Calf survival followed a similar trend to

pregnancy but was highly variable and was also lowest for residents (x = 0.0704, 95% CRI = 0.00–0.316), followed by the western tactic (x = 0.153, 95% CRI = 0.00591–0.450), and highest in the eastern tactic (x = 0.202, 95% CRI = 0.00231–0.731) (Tables 1–4).

# DISCUSSION

We found evidence for most of the predictions of Ideal Free Distribution to support the IFD as a framework for explaining the maintenance of different migratory tactics within a partially migratory large herbivore population. Further, our results are among the first to explicitly link switching of migratory tactics to fitness benefits, filling a much-needed gap in knowledge of partial migration (Bolger et al., 2008; Gaillard, 2013). The migratory switching rates we observed toward the tactic of higher fitness suggests the migrant to resident ratio in migratory flexible populations is dictated not only by the counteracting density-dependent vital rates resulting in a population level stable state (Cressman & Křivan, 2006; Kaitala et al., 1993; Lundberg, 1987) but also by individuals attempt to maximize fitness. Under IFD, we expected equal fitness among strategies, which was







**FIGURE 3** (a) The mean year-to-year transition probability  $\varphi$  of elk switching migratory tactics from the eastern (gray), resident (yellow), and western (blue) tactic. No switching was observed between east to west tactics. (b) Probability of switching to an alternate migratory tactic for resident, eastern, and western migrant elk as a function of the predicted fitness (lambda,  $\lambda$ ) derived from the Integrated Population Model, at Ya Ha Tinda, 2002–2019

supported, despite there being some differences in vital rates especially at high densities. Density dependence in demography as a mechanism to facilitate tactic selection is consistent with IFD (Kaitala et al., 1993). We found density dependence in pregnancy rates of resident, as well as some weak evidence of density-dependent adult survival. Finally, our most exciting result is that individual elk changed their choice of migratory tactic in a manner that is consistent with this key prediction of the IFD, that is they switched to the migratory tactic with the highest fitness. Recent studies have revealed migratory flexibility in large herbivores, but our results demonstrate that this flexibility may be driven by individuals' search for the ideal, free home. Thus, the classic theory of IFD may be of value in explaining and uncovering the dynamics of partially migratory taxa.

We found evidence for winter range, densitydependent vital rates providing a stimulus for migratory tactic selection, which resulted in IFD of migratory tactics. Pregnancy rates of residents declined at high densities, a classic indicator of forage-limited density dependence (Bonenfant et al., 2009; Stewart et al., 2005). Lower pregnancy rates at higher density provided an incentive to switch migratory tactics because migrant



**FIGURE 4** Posterior distribution and 95% credible intervals of the geometric mean of population growth rate (lambda,  $\lambda$ ) of the eastern, western, and resident migratory tactics



**FIGURE 5** Estimated number of female elk and 95% credible intervals of the eastern, resident, and western migratory tactics of the Ya Ha Tinda elk population (2002–2019)

females were exposed to higher forage quality on the summer range than residents (Hebblewhite & Merrill, 2009) reflected in higher diet quality (Hebblewhite & Merrill, 2009; Normandeau et al., 2020). The reason that winter-range density dependence occurred only for the resident tactic was because higher summer forage quality of migrants affected the probability of pregnancy in the subsequent year and is essential for temperate ungulates to regaining body fat and body condition following lactation (Cook et al., 2004, 2010). As a result, resident females were expected to exhibit stronger density dependence than migrants. The density-dependent effects on pregnancy rates suggests that, at high densities,

migration was the better tactic as females require higher quality forage in summer to recover from the demands of lactation (Eggeman et al., 2016). But at low densities, remaining a resident in a predictable and known landscape with lower predation risk on adults (Hebblewhite & Merrill, 2009) yielded higher expected fitness (Hebblewhite et al., 2018, Figure 5). The density-dependent effect of pregnancy in our study was different than pike, where densitydependent survival of adults was the driver of Haugen et al. (2006)'s ideal free pike findings. Given the high predation rates in our study area (Hebblewhite et al., 2018; Hebblewhite & Merrill, 2011), weak density-dependent responses (particularly in adult female survival) is expected if predators keep the elk population below winter range carrying capacity (Hebblewhite et al., 2018; Wang et al., 2009). The resident tactic had the highest adult survival rate due to reduced predation risk (Hebblewhite & Merrill, 2011), which appears to be the primary driver of lambda. These patterns we observed are consistent with trends in the loss of migratory behavior among temperate ungulates at least in North America (e.g., Middleton et al., 2011).

Our clearest and strongest support of the IFD was the evidence for clear facultative switching in response to differences in fitness between migratory tactics. Cressman and Křivan (2006) demonstrated differential density dependence leads to IFD in theoretical population modeling, but for IFD to be behavioral, evidence of switching toward a tactic of higher pay-off is necessary. We found that switching rates were positively correlated with the difference in fitness between migratory tactics in the previous year. This result is contrary to the results **TABLE 1** Beta coefficients, standard error (SE), and 95% confidence limits of the generalized linear models (GLM) model for effect of migratory tactic and elk abundance (centered at x = 805 and scaled by  $\sigma = 268$ ) in winter and their interaction on adult female survival at the Ya Ha Tinda population, Alberta, Canada, 2002–2019

	Covariate and			95% CI			
Covariate	migration tactic	β	SE	Lower	Upper	р	
Migratory tactic	R	0.935	0.00153	0.932	0.938	< 0.001	
	Е	0.843	0.00153	0.841	0.847	< 0.001	
	W	0.850	0.00153	0.847	0.853	< 0.001	
Migratory tactic $\times$ Abundance	R	-0.00401	0.00155	-0.00711	-0.00090	0.013	
	Е	0.00019	0.00155	-0.00292	0.00329	0.904	
	W	-0.00037	0.00155	-0.00348	0.00273	0.811	

Note: Migratory tactics are resident (R), eastern (E), and western (W).

**TABLE 2** Beta coefficients, SE, and 95% confidence limits of the GLM model for effect of migratory tactic and elk abundance (centered at x = 805 and scaled by  $\sigma = 268$ ) in winter and their interaction on calf survival rates (male and female) at the Ya Ha Tinda population, Alberta, Canada, 2002–2019

	Covariate and			95% CI			
Covariate	migration tactic	В	SE	Lower	Upper	р	
Migratory tactic	R	0.05085	0.01779	0.01528	0.08643	0.5729	
	Е	0.16704	0.01779	0.13146	0.20262	< 0.01	
	W	0.13619	0.01779	0.10062	0.17176	< 0.01	
Migratory tactic $\times$ Abundance	R	0.02952	0.01795	-0.00638	0.06543	0.107	
	Е	-0.00461	0.01795	-0.04052	0.03129	0.798	
	W	-0.00902	0.01795	-0.04493	0.02688	0.617	

**TABLE 3** Beta coefficients, SE, and 95% confidence limits of the GLM model for effect of migratory tactic and elk abundance (centered at the mean and scaled by  $\sigma$ ) on pregnancy rates of adults at the Ya Ha Tinda population, Alberta, Canada, 2002–2019

				95% CI		
Covariate	Migration tactic	β	SE	Lower	Upper	р
Migratory tactic	R	0.852	0.00879	0.834	0.969	< 0.001
	Ε	0.952	0.00879	0.934	0.870	< 0.001
	W	0.911	0.00879	0.893	0.928	< 0.001
Migratory tactic $\times$ Abundance	R	-0.060	0.00887	-0.0774	-0.0419	< 0.001
	Е	0	0.00887	-0.0180	0.0174	0.972
	W	-0.003	0.00887	-0.0208	0.0147	0.734

of Mosser et al. (2009) and Green et al. (2015) who found dispersal and migration followed the ideal despotic and not ideal free distribution in African lions (*Panthera leo*) and American Dippers (*Cinclus mexicanus*). Both studies found dispersal of territorial lions and migration of Dippers was toward areas of lower fitness, a key prediction of the ideal despotic distribution theory (Fretwell & Lucas, 1970) and a common source–sink dynamic observed in territorial systems (Pulliam & Danielson, 1991). Territoriality and direct competition are not usually associated with large herbivores; however, in an interesting exception, Hurley et al. (2011) found that density-dependent survival of mule deer fawns was driven by competition for enemyfree space and not forage, supporting the application of density-dependent habitat selection to herbivores.

Individuals in our study switched to migratory tactics of higher fitness, suggesting that individuals acted in an

TABLE 4	Beta coefficients,	SE, and 95% confidence	e limits of the	GLM model for	effect of	migratory	tactic and	abundance (	(centered	at
x = 805 and sc	aled by $\sigma = 268$ ) o	n tactic switching rates	s at the Ya Ha	Tinda populatio	on, Alber	ta, Canada	, 2002–201	9		

				95% CI		
Covariate	Migration tactic	β	SE	Lower	Upper	р
Migratory tactic	R	0.10822	0.01476	0.07868	0.13775	< 0.01
	Е	0.07352	0.01476	0.04399	0.10306	0.132
	W	0.20939	0.01476	0.17985	0.23892	< 0.001
Migratory tactic $\times$ Abundance	R	-0.00653	0.01491	-0.03636	0.02329	0.663
	Е	0.04865	0.01491	0.01882	0.07848	< 0.01
	W	-0.00658	0.01491	-0.03641	0.02324	0.661

ideal manner and switched to migratory tactics that increased their individual fitness on a year-to-year basis (Figure 3b). While this suggests the population may not have been at an equilibrium stable state as a result of the IFD the empirical test of the IFD by Haugen et al. (2006) similarly found that the net dispersal rate between two pike populations was still toward the population with higher intrinsic fitness, even after the population reached an equilibrium stable state. If individuals in IFD attempt to switch toward the tactic of higher intrinsic fitness once fitness is equalized, this suggests the resident tactic had higher intrinsic fitness despite the observed fitness between the tactics being equal (Figure 3a).

One of the primary predictions of the IFD is that the fitness of individuals between migratory tactics is equal, despite differential density-dependence in vital rates, which we observed over a 70% decline in abundance. However, if the tactics had different forms of densitydependence, this means density and thus tactic selection was dynamic during our study. The density-dependent switching rates of residents to eastern migrants supports this observation, as higher switching rates occurred at higher densities. However, the slightly lower fitness of both migrant strategies suggests that, as abundance declined, the density dependence of the resident tactic (through pregnancy) weakened. Unfortunately, our study began after the population began to decline so we did not observe the period when the population increased. Under increasing population abundance, we might instead have predicted winter-range density dependence to result in greater switching to migratory individuals, such as was observed in our study area at much higher densities in the late 1970s (Hebblewhite et al., 2006). In our system, we believe that at low densities, the resident tactic had higher fitness. But if densities increased, there would be a density where the fitness of residents would be less than the migrant tactic, after which individuals would be expected to switch to the migratory tactic. A similar relationship would explain partial migration in Serengeti

wildebeest, where the fitness of residents may quickly decline with density making migration the better tactic resulting in small proportion of residents in the population (Hopcraft et al., 2015). Our assessment reveals that the IFD could be applied to other partially migratory populations where tactic switching occurs to understand the population dynamics and consequences of changes in density to partially migratory populations.

Contrary to some ungulate species that show little to no variation in migratory behavior (Sawyer et al., 2019), elk and many other partially migratory ungulates demonstrate migratory plasticity and switch migratory tactics throughout their life (Cagnacci et al., 2011; Festa-Bianchet, 2013; Morrison & Bolger, 2012; Mysterud et al., 2011). Large herbivores may be able to assess the condition or reproductive status of a migratory tactic from year to year and make choices based on their expected fitness outcomes. For the fitness consequences of a tactic to be perceived, an individual must either (1) observe the benefits directly through trial and error under the winstay, lose-leave process (Switzer, 1993) or memory-based decision processes; (2) observe the success of other individuals in other tactics; or (3) rely on cultural transmission of tactic success (perhaps through relatives). In a predictable environment, the knowledge of fitness consequence can be learned quickly, and fitness maximized through individual experience and the win-stay, lose-leave decision process (Chalfoun & Martin, 2010; Switzer, 1993). For example, after a sequence of unsuccessful reproduction attempts, an individual may opt to switch migratory tactics. Inferring the fitness consequence of a decision may take many years of individual trial and error given stochasticity, and thus, knowledge may not be ideal nor instantaneous. In these scenarios, individuals may use conspecific cues to infer the benefits of tactic selection. Indeed, earlier results from our system demonstrate that while some individuals switch every year, on average individual elk switch at a rate of 0.16/year (Eggeman et al., 2016), like other ungulate species (Berg et al., 2019).

These observed switching rates support the hypothesis that the decision to switch may be a multi-year process. For example, individuals gain information about the success of conspecifics by mingling or prospecting on the breeding grounds (Boulinier & Danchin, 1997; Brown et al., 2000; Cadiou et al., 1994), which may intensify when group size increases in higher predation risk systems (Merrill et al., 2020; White et al., 2012).

Regardless of our uncertainty about exactly how elk seem to be making "ideal free" decisions regarding switching between migratory tactics in our system, our results clearly indicate the population-level implications of considering ideal free dynamics in the maintenance of partial migration. Our results echo other recent studies that suggest that migration itself may be a polymorphic behavior in large herbivores (Gaudry et al., 2015), where the choice to migrate is determined by differential costs and benefits of different tactics, mediated by differential density dependence. We once again call for the importance of long-term studies when studying migration and long-lived ungulates as well as the need to monitor individual reproductive success to determine the mechanisms that result in these decision-making processes (Bolger et al., 2008; Clutton-Brock & Sheldon, 2010).

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#### **CONFLICT OF INTEREST**

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data (Martin et al., 2020) are available on Dryad at https://doi.org/10.5061/dryad.6wwpzgmw7. The jags IPM model (Martin, 2021b) is available on Zenodo at https:// doi.org/10.5281/zenodo.5717331.

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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