



Attributes of seasonal home range influence choice of migratory strategy in white-tailed deer

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Partial migration is a common life-history strategy among ungulates living in seasonal environments. The decision to migrate or remain on a seasonal range may be influenced strongly by access to high-quality habitat. We evaluated the influence of access to winter habitat of high quality on the probability of a female white-tailed deer (*Odocoileus virginianus*) migrating to a separate summer range and the effects of this decision on survival. We hypothesized that deer with home ranges of low quality in winter would have a high probability of migrating, and that survival of an individual in winter would be influenced by the quality of their home range in winter. We radiocollared 67 female white-tailed deer in 2012 and 2013 in eastern Washington, United States. We estimated home range size in winter using a kernel density estimator; we assumed the size of the home range was inversely proportional to its quality and the proportion of crop land within the home range was proportional to its quality. Odds of migrating from winter ranges increased by 3.1 per unit increase in home range size and decreased by 0.29 per unit increase in the proportion of crop land within a home range. Annual survival rate for migrants was 0.85 ($SD = 0.05$) and 0.84 ($SD = 0.09$) for residents. Our finding that an individual with a low-quality home range in winter is likely to migrate to a separate summer range accords with the hypothesis that competition for a limited amount of home ranges of high quality should result in residents having home ranges of higher quality than migrants in populations experiencing density dependence. We hypothesize that density-dependent competition for high-quality home ranges in winter may play a leading role in the selection of migration strategy by female white-tailed deer.

Key words: competitive release hypothesis, habitat quality, home range, *Odocoileus virginianus*, partial migration, survival

In regions where habitat quality varies by season and a migratory species experiences some form of density dependence, the presence of partial migration (i.e., some individuals migrate, whereas others do not) in a population is likely the rule rather than the exception (Lundberg 1988; Taylor and Norris 2007; Chapman et al. 2011; Avgar et al. 2014). In populations where partial migration occurs, migratory behaviors of individuals fall along a continuum ranging from resident to migrant (Ball et al. 2001; Cagnacci et al. 2011). A commonly hypothesized explanation for this pattern is that partial migration is a frequency-dependent, evolutionarily stable strategy (ESS—Lundberg

1987, 2013; Kaitala et al. 1993; De Leenheer et al. 2017), where individuals choose to remain resident or migrate such that their fitness might be maximized.

Individuals at the extremes of the behavioral continuum consistently make the same decision regarding migration, whereas individuals between the extremes may or may not migrate throughout their lifetimes depending on intrinsic (e.g., age, social status, competitive ability—Kaitala et al. 1993; Nathan et al. 2008; Chapman et al. 2011) and extrinsic (e.g., food availability, breeding opportunities, predation risk—Hebblewhite and Merrill 2007; Hebblewhite et al. 2008; Myrsterud et al.

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2011) conditions. Response to external conditions can also depend on population density; the competitive release hypothesis states that in populations experiencing density-dependence, competition should result in residents using higher-quality habitat than migrants (Gauthreaux 1982). Quantifying how proximate conditions affect the decision to migrate allows prediction of when and if an individual will migrate, and by extension the migratory proportion of a population.

Habitat quality, a measure of the presence of resources needed for survival and reproduction (Hall et al. 1997), can represent local conditions influencing the fitness and behavior of an individual. Reproductive success and survival of juveniles and adults can increase with habitat quality (Gaillard et al. 2000; Pettorelli et al. 2003; Bishop et al. 2009). The distribution and size of home ranges and territories also can be governed by habitat quality (McLoughlin et al. 2000; Mitchell and Powell 2007; Owen-Smith et al. 2010). Habitat quality influences local carrying capacity and population density, and thus can be the basis for density-dependent competition for resources (Dhondt 2010). Variability in components of habitat quality (e.g., topography, snow cover, forest patch density, and size) has been shown to be associated with the decision of an individual to migrate or remain resident (Cagnacci et al. 2011; Grovenberg et al. 2011).

In environments that are spatially and temporally variable, the decision to migrate has been shown to have both positive and negative consequences for survival (Nicholson et al. 1997). Basic migration theory (Lack 1954) suggests that if the fitness costs of remaining in a seasonal range outweigh the benefits, then natural selection will favor movement to another seasonal range. Conversely, if the costs of moving outweigh the benefits of staying, then natural selection will favor an animal remaining in its original seasonal range. These costs and benefits change depending on local ecological conditions and directly affect the selection of a migration strategy by an individual. Thus, migration has the potential to decrease survival because of increased energy expenditures and exposure to predation (Nicholson et al. 1997) or increase survival by enhancing availability of resources, reducing energy expenditure, and reducing vulnerability to predation (Avgar et al. 2014). Over time, survival of migrants and residents within a partially migratory population should be generally equivalent because individuals choose seasonal home ranges that minimize risks to survival, depending on local conditions (Lack 1968).

Partial migration has been documented in most northern cervids, including white-tailed deer (*Odocoileus virginianus*—Sabine et al. 2002; Nixon et al. 2008; Grovenberg et al. 2011), mule deer (*Odocoileus hemionus*—Brown 1992; Nicholson et al. 1997), moose (*Alces alces*—Ball et al. 2001; White et al. 2014), and elk (*Cervus canadensis*—Boyce 1989). Of these cervid species, white-tailed deer have the widest geographical distribution (Heffelfinger 2011), resulting in individuals within a population having seasonal home ranges across the spectrum of habitat quality. White-tailed deer populations are partially migratory in the presence of strong seasonality, with many individuals that change between behaviors over the course of their lifetimes (Nelson 1995; Sabine et al. 2002; Fieberg et al.

2008). Numerous studies have investigated migration in white-tailed deer (Verme 1973; Van Deelen et al. 1998; Nelson et al. 2004; Brinkman et al. 2005) with a primary focus on timing of migration. Fewer studies (Nixon et al. 2008; Grovenberg et al. 2009) have evaluated the proximate conditions that influence the decision of an individual to migrate. Juvenile experience has been suggested as one influence on the migratory strategy individuals adopt as adults (Pac et al. 1991; Nelson 1998; Nixon et al. 2008) but it does not explain switching between migratory strategies by individuals observed in some populations of white-tailed deer (Nelson 1998; Fieberg et al. 2008). Competition where parturition habitat is limited also has been suggested as an influence on the decision of an individual to migrate (Nixon et al. 2008).

Our objectives were to evaluate whether spring migration by female white-tailed deer could be predicted by the quality of their home ranges in winter, and to quantify the effects of this decision on survival. Defining habitat quality is notoriously challenging (Hall et al. 1997; Johnson 2007; Mitchell and Hebblewhite 2012), because environmental conditions contributing directly to survival and reproduction can be difficult to discern or measure empirically. The broad distribution and generalist food habits of white-tailed deer make it difficult to find a consensus of what constitutes high-quality habitat, although agricultural and riparian areas are consistently associated with their selection of habitat. Numerous studies have found an inverse, density-dependent relationship between home range size and habitat quality (McLoughlin et al. 2000; Mitchell and Powell 2007; Gaudry et al. 2015). Therefore, we tested the hypothesis that deer with low-quality home ranges in winter (i.e., large, containing a small proportion of high-quality land cover types) would have a higher probability of migrating than those occupying high-quality home ranges in winter (i.e., small, containing a large proportion of high-quality land cover types). We also expected the quality of seasonal home range to influence survival of individuals. Therefore, we tested the predictions that 1) migrants would have a lower winter survival rate than residents, and 2) that survival rates for migrants and residents would be approximately equal in summer because both groups have access to summer ranges of comparable quality. We assumed that home ranges in summer would be of comparable quality due to the general increase in available resources during the summer season and the larger portion of the landscape available for exploitation during the summer. We expected the larger portion of available landscape to allow individuals on summer ranges to expand their home range size if necessary to compensate for any differences in the nutritional value of available forage within a particular home range.

MATERIALS AND METHODS

Study area.—Our study area included 2 game management units (117 and 121), located near Chewelah, Washington (48°29'N, 117°72'W). The study area boundary on the north was the United States and Canadian border. The Columbia River formed the western boundary and the Pend Oreille River

the eastern boundary. The southern boundary was the Spokane River west of U.S. highway 395 and U.S. Route 2 to the east. Topographically, the study area included 2 mountain ranges, the Abercrombie and Huckleberry Mountains, which make up the southern terminus of the Selkirk mountain range and 3 river valleys. Mean annual precipitation was 45.6 cm. Average temperatures for winter were -1.7°C and 19.4°C for summer (Office of Washington State Climatologist 2012). A winter severity index for deer (DelGiudice et al. 2002) calculated for our study area showed that this study took place during 2 of the mildest winters over a 12-year period. The study area consisted of 57.6% privately owned land, 25.6% U.S. Forest Service owned land, and ownership of the remaining 16.8% was split between other federal, state, and tribal agencies (Washington Department of Fish and Wildlife 2010). The dominant land cover was coniferous forest (68.2%). The next largest cover types were shrub and brush land (11.6%) and grassland-pasture (6.6%). The remaining 13.6% was divided between cultivated crops, wetlands, urban-rural development, and broadleaf forest (Washington Department of Fish and Wildlife 2010).

Capture and handling.—We captured white-tailed deer between 1 January and 4 March in 2012 and 2013 using modified Clover traps (Clover 1956). We pre-baited and baited the trapping area and traps with alfalfa hay. Upon capture, we blindfolded and physically restrained deer for processing. We placed numbered ear tags (Y-Tex Corporation, Cody, Wyoming) in the right ear of each deer. We monitored physical stress via rectal temperature and used snow to cool the animal if temperature exceeded 40°C . We assigned deer to 1 of 3 age categories (adult, yearling, juvenile) based on tooth wear and replacement (Severinghaus 1949). We outfitted adult (≥ 2.5 years old) and yearling (1.5–2.5 years old) female deer with either GPS or VHF radiocollars, and we equipped juveniles (< 1.5 years old) with VHF ear tags (Advanced Telemetry Systems, Inc., Isanti, Minnesota). We followed University of Montana (Animal Use Protocol 050-11) animal handling protocols and the guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes et al. 2016).

Migratory status.—We recorded locations for GPS-collared deer every 4 h starting at 00:00 on even-numbered days and 01:00 on odd-numbered days from January 2012 to January 2014. We located deer with VHF collars from the ground every other week and estimated their location using triangulation (Nams 2006). VHF-collared deer also were located by fixed-wing aircraft, depending upon available resources and favorable flying conditions, and the location was recorded using GPS.

We used net squared displacement (NSD), the straight-line distance from a single starting location to all subsequent locations for an individual, to define migrant and resident deer (Bunnfeld et al. 2011; Singh et al. 2012). We calculated NSD in the R (R Development Core Team 2012) package *adehabitatLT* (Calenge 2006) using the *ltraj* function. We used the capture site as the point of origin for the linear measurements used to calculate NSD (Fryxell et al. 2008; Mysterud et al. 2011). We defined migration as a seasonal movement that results in nonoverlapping ranges (Ball et al. 2001). We assigned deer to migrant or resident

categories for analysis based on a visual inspection of NSD graphs, seasonal home ranges generated from GPS, and VHF location data (Mysterud et al. 2011). Female white-tailed deer are less likely to disperse than males (Nelson 1993; DeYoung 2011) and a portion of the females that disperse has been observed returning to their traditional winter range (Nelson and Mech 1992); consequently, we counted any deer observed moving to a nonoverlapping home range a single time as a migrant (Fieberg et al. 2008). We treated annual movement patterns for deer monitored for more than 1 year as independent observations. We assumed that the decision to migrate each year was independent from year to year. This assumption was supported by the study conducted by Fieberg et al. (2008) which showed that the longer an individual white-tailed deer is observed the more likely it becomes that it will change its migratory behavior. We tested for the effects of pseudoreplication by conducting a post hoc analysis that used a model for predicting migration strategy that included random intercepts for each annual observation of an individual. The outcome of this analysis was not significantly different from the original results; therefore, we concluded that pseudoreplication was not an issue in this case.

We defined the dates of seasonal home ranges for migrants and residents using life-history traits and movement data. We divided each year into 2 seasons: summer (parturition and pre-weaning) and winter (reduced forage availability and reduced metabolism). We determined the beginning dates for seasonal home ranges for migrants on an individual basis by using NSD, GPS, and VHF locations. We defined home ranges in winter from the 1st location where we observed no further migratory movements to the last location before movement toward summer range (Nelson et al. 2004). We designated resident dates for home range in winter by selecting the date at the midpoint between the mean start and end dates of migration events in both the fall and spring (Grovenburg et al. 2011). We estimated winter and summer home ranges for each GPS-collared deer using a 95% fixed kernel (Worton 1989) contour estimated in R package *adehabitatHR* (Calenge 2006). We used the reference bandwidth (h_{ref}) as the smoothing parameter.

Probability of migration.—We determined the composition of habitats in winter home ranges using remotely sensed data using only locations collected from GPS-collared individuals. We assessed a total of 45 winter home ranges estimated using data collected from 26 GPS-collared individuals over 3 winters. We did not use winter home ranges generated from VHF-collared deer due to the relatively small number of locations for those individuals and the resulting coarse-grained estimates of their home ranges in winter. We obtained land cover data from Landfire 1.2.0 (Landfire 2014) and collapsed the approximately 130 vegetation classification categories contained in the Landfire GIS layer for the study area into 12 general land cover types. These 12 land cover types represented the majority of the landscape and were ranked on their ability to fulfill some biological requirement for white-tailed deer such as food or cover based on a review of the literature (Table 1; Crawford and Marchinton 1989; Miranda and Porter 2003; Hewitt 2011; Stewart et al. 2011). We used ArcMap 10.0 (ESRI 2010) to calculate the proportion of each land cover

type in each home range. We conducted a univariate regression and tested for correlation between land cover types. We reduced the number of land cover types used to construct our a priori set of models to estimate the probability of migrating based on the significance of each land cover type from the univariate regression ($P < 0.001$) and its correlation with other land cover types ($P < 0.7$). The reduced number of land cover types (2) were used to construct 11 models (Table 2) to estimate the probability of migrating using different combinations of home range size in winter, the proportion of cropland in the home range in winter, and the proportion of pasture in the home range in winter.

Survival estimation.—Annual and seasonal survival rates were estimated from encounter histories created for deer with a known migration strategy. These encounter histories included both GPS- and VHF-collared individuals ($n = 65$). We used a known-fate modeling approach to estimate survival. We included 2 categorical covariates, season and migratory strategy, in the model to estimate seasonal and annual survival for migrants and residents.

Model analysis.—We employed a Bayesian statistical framework to conduct analysis of all models. We used JAGS 3.4.0 (Plummer 2003), R package R2jags (Su and Yajima 2015), R package rjags (Plummer 2016), and R package jagsUI (Kellner 2016). We standardized the size of home ranges and land cover variables to facilitate analysis within the JAGS program and incorporated them into the migration prediction model using a logit link function (Kéry and Schaub 2012). We employed uninformative priors drawn from a uniform distribution. We assessed convergence using trace plots generated in R package mcmcplots (Curtis 2015), the Gelman–Rubin diagnostic test in R package coda (Plummer et al. 2006), and the R package jagsUI. We conducted 100,000 iterations and discarded the initial 5,000 iterations for the burn-in period. We used 5 chains with different initial values to ensure that initial values did not influence estimates. We ranked models using Deviance Information Criterion (DIC—Spiegelhalter et al. 2002), and considered models within 2 DIC units to be equally as likely. We used the “f” output from jagsUI, a measure of the proportion of the

posterior distribution that had the same sign (positive or negative) as the mean value of the parameter estimate, as a measure of the confidence in the parameter estimate. We then tested the model fit of our top model for predicting migration strategy by using k -fold cross-validation (Boyce et al. 2002). We randomly selected 70% of the observations to form a training set and used the remaining proportion of the data as the test set (Guyon 1997; $k = 100$). We evaluated model performance by comparing the mean predictive error (i.e., the proportion of individuals whose migration strategy was incorrectly predicted by the model) from this analysis to the predictive error for the model generated from the entire data set.

RESULTS

We captured deer at 7 locations within the study area and radio-collared 69 females during January, February, and March of 2012 ($n = 30$) and 2013 ($n = 39$) including 37 adults, 20 yearlings, and 12 juveniles. We fitted deer with 37 GPS collars (21 adults, 16 yearlings), 20 VHF collars (16 adults, 4 yearlings), and 12 VHF ear tags (juveniles). Juveniles and yearlings that survived longer than 1 year were included as yearlings and adults in the following year. We used GPS locations to calculate 84 observed home ranges for winter 2011–2012 ($n = 10$), summer 2012 ($n = 10$), winter 2012–2013 ($n = 24$), summer 2013 ($n = 23$), and winter 2013–2014 ($n = 17$). We recorded 39 migratory movements during spring 2012 ($n = 7$), fall 2012 ($n = 5$), spring 2013 ($n = 19$, 4 of which were deer observed for a 2nd year), and fall 2013 ($n = 8$, 4 of which were deer observed for a 2nd year). No collared deer observed for > 1 year switched migratory strategies between years.

We estimated the probability of migration from 74 observations of annual movement patterns that included both migrants ($n = 44$) and residents ($n = 30$), from 42 individual deer. In winter, the mean size of observed home ranges for migrants ($\bar{x} = 343.6$ ha, $SD = 91.49$) was larger than for residents ($\bar{x} = 207.2$ ha, $SD = 75.94$). The top model for estimating the probability of an individual migrating from winter range was a function of the size of the home range in winter and the proportion of cropland within the home range in winter. The size of home ranges

Table 1.—Relative value of land cover types to meet biological requirements of white-tailed deer (*Odocoileus virginianus*) for food and cover. Values assigned based on: Crawford and Marchinton (1989), Rothley (2001), Miranda and Porter (2003), Grovenburg et al. (2011), Hewitt (2011), and Stewart et al. (2011).

Cover type	Food	Cover
Water	Low	Low
Developed	Medium	Medium
Crop	High	Low
Pasture	High	Medium
Grassland	High	Low
Sparse vegetation	Low	Low
Aspen	Medium	Medium
Closed canopy conifer	Low	High
Open canopy conifer	Medium	Medium
Shrub	High	High
Steppe	Low	Low
Riparian	High	High

Table 2.—Candidate models for estimating an individual’s probability of migrating from winter range. WRS—home range size in winter; crop—proportion of cropland in winter home range; pasture—proportion of pasture in winter home range.

Models
crop
pasture
WRS
crop + pasture
crop + WRS
pasture + WRS
crop + pasture + WRS
crop + WRS + WRS * crop
crop + pasture + WRS + WRS * pasture
crop + pasture + WRS + crop * pasture
crop + pasture + WRS + WRS * crop

in winter was associated positively with the probability of migration, with the odds of migration increasing by 3.11 (95% credible interval [CRI] = 0.97–14.54) for each unit increase in standardized home range size (Fig. 1). The proportion of cropland in a home range in winter was associated negatively with the probability of migration, with the odds of migration decreasing by 0.29 (95% CRI = 0.10–0.69) for each unit increase in the standardized proportion of cropland (Fig. 2). The mean size of observed home ranges in summer for migrants (\bar{x} = 232.1 ha, SD = 131.4) was larger than for residents (\bar{x} = 102.9 ha, SD = 113.8). When we removed estimates for a single outlying migrant (1,568.08 ha), home range size in summer for migrants (\bar{x} = 137.64 ha, SD = 39.52) was similar to residents. The mean predictive error (0.26, SD = 0.103) from the cross-validation model evaluation did not differ from the predictive error from the model based on the full data set (0.222).

We estimated annual and seasonal survival for 44 migrant and 21 resident female deer, which included 10 individuals observed over multiple years. The model used for estimating survival was a function of migration strategy and season. Seasonal survival was nearly identical between migrants and residents (Table 3), as was annual survival (migrants: 0.85, SD = 0.05; residents: 0.84, SD = 0.09).

DISCUSSION

A central question in the study of animal populations that migrate is why some individuals migrate, while others do not. Basic migration theory (Lack 1954) suggests that if the fitness costs of remaining in a seasonal range outweigh the benefits,

then natural selection will favor movement to another seasonal range. Conversely, if the costs of moving outweigh the benefits of staying, then natural selection will favor an animal remaining in its original seasonal range. Partial migration is a life-history strategy employed by white-tailed deer populations in regions of their distribution that experience strong seasonality. We sought to identify how access to winter habitat of high quality influences the decision of a female white-tailed deer to migrate and to quantify the effect of migration on survival. In support of predictions stemming from theory associated with partial migration, quality of home ranges in winter was associated negatively with the propensity to migrate in spring. Nevertheless, in contrast to our expectations, migratory strategy was unrelated to seasonal or annual survival.

Our results support the competitive release hypothesis as a possible explanation for the mechanism underlying the decision of female white-tailed deer to migrate or not. This hypothesis states that competition for a limited amount of home ranges of relatively high quality should result in residents having home ranges of higher quality than migrants in populations experiencing density dependence, and has been documented in red deer (Myerud et al. 2011) and moose (White et al. 2014). Previous work has attributed the decision of female white-tailed deer regarding migration to juvenile experience (Nelson 1998; Nixon et al. 2008), competition for parturition sites (Nixon et al. 2008), or forest patch attributes (Grovenburg et al. 2011). Our finding that female white-tailed deer on relatively poor-quality home ranges in winter were more likely to migrate is consistent with the competitive release hypothesis. We therefore hypothesize that the decision to migrate for the deer we observed is

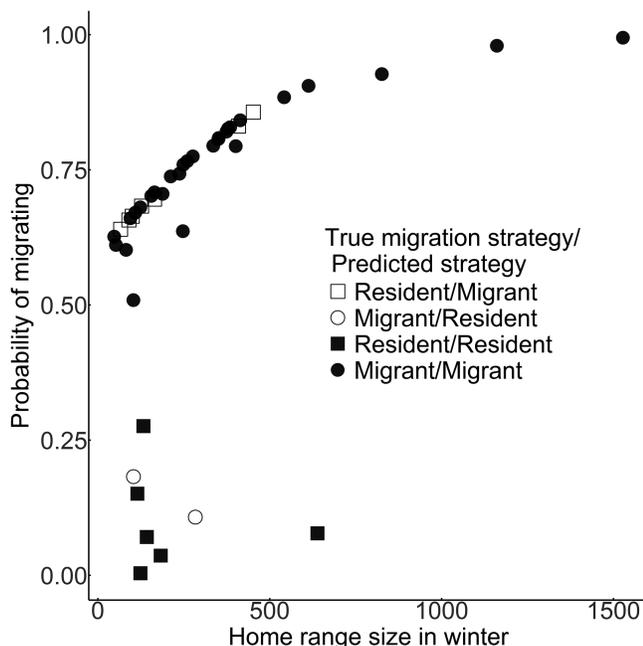


Fig. 1.—Predicted probability of migration as a function of an individual white-tailed deer's (*Odocoileus virginianus*) home range size in winter. Closed shapes indicate individuals whose true migration strategy was correctly predicted by the top model and open shapes indicate individuals whose true migration strategy was incorrectly predicted by the top model.

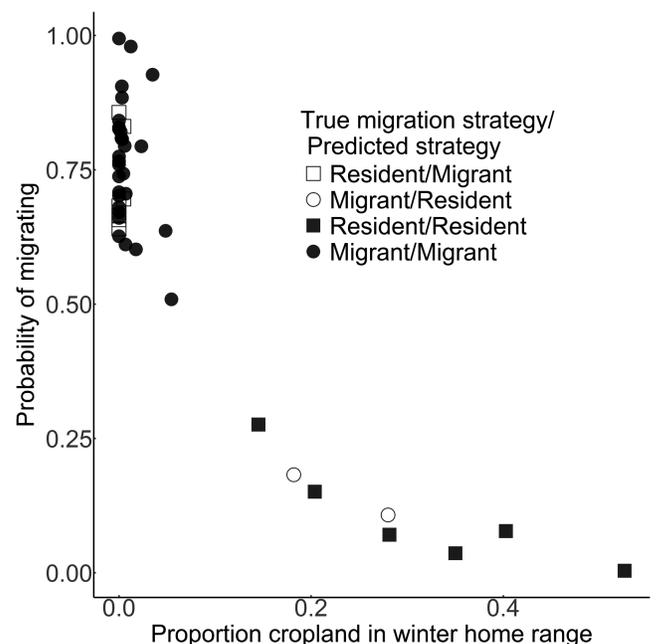


Fig. 2.—Predicted probability of migration as a function of the proportion of cropland in a home range in winter. Closed shapes indicate individual white-tailed deer (*Odocoileus virginianus*) whose true migration strategy was correctly predicted by the top model and open shapes indicate individuals whose true migration strategy was incorrectly predicted by the top model.

Table 3.—Seasonal survival estimates for migrant and resident female white-tailed deer (*Odocoileus virginianus*) in Stevens County, Washington, 2012–2014. Winter consists of the months December through April. Summer consists of the months from May to November. CRI = credible interval.

Season	Migrant			Resident		
	Mean	SD	CRI	Mean	SD	CRI
Winter	0.968	0.02	0.91–0.99	0.961	0.03	0.88–0.99
Summer	0.88	0.05	0.77–0.96	0.867	0.072	0.7–0.97

based on density-dependent competition for home ranges in winter. If true, residents inhabit home ranges of high quality year-round, whereas migrants are excluded by density-dependent competition from these home ranges in winter. Therefore, migrants must move to areas where competition for high-quality habitat is presumably less to find summer ranges that are comparable in quality to resident home ranges. Upon return to winter range, migrants again compete for high-quality home ranges; their success in part determines the decision to migrate the following summer.

Our results also have implications for predicting the switching of migration strategies by individuals within partially migratory populations. Annual variation in competitive ability of individuals, population density, food productivity, and winter severity might explain how decisions to migrate vary among individuals and between years (Nelson 1998; Van Deelen et al. 1998; Fieberg et al. 2008). The results of this study suggest that competition for high-quality home ranges, during the portion of the year when the entire population shares a range, may influence the decision of an individual to migrate or remain resident. It follows that the proportion of migrants in a partially migratory population should be inversely related to availability of high-quality habitat on the shared range. We hypothesize that as the amount of available resources change, the degree of competition for a home range of high quality should fluctuate (Mysterud 2000). We predict that a relatively large proportion of conditional migrants should remain resident when resources are abundant and intensity of competition is reduced. Conversely, we predict that a relatively large proportion of conditional migrants should migrate when resources are reduced and intensity of competition is increased. Using a measure of home range quality, such as home range size, can then be used to predict changes in the ratio of migrants to residents in a population and can inform conservation of partially migratory populations by guiding management of seasonal ranges, forecasting amount and distribution of harvest, and predicting the spread of disease (Grovenburg et al. 2011).

We did not measure competition directly but assumed that deer competed for high-quality home ranges for our analyses. The size of a home range has been shown to be a density-dependent measure of habitat quality (McLoughlin and Ferguson 2000; Mitchell and Powell 2007); variation in size of home ranges can represent the outcome of competition (i.e., less competitive individuals had large, low-quality home ranges). By using home range size, we were able to more comprehensively test the influence of habitat quality on the decision to migrate than if we had used only components of home range quality.

Consistent with the notion that partial migration is an ESS (i.e., an individual chooses to remain resident or migrate to maximize its fitness), Lack (1968) previously argued that the survival of migrants and residents in a partially migratory population should be generally equivalent over time. Consistent with this hypothesis (and similar to other work on white-tailed deer—Nixon et al. 2008), we observed similar annual and seasonal survival between deer pursuing different migratory strategies, suggesting that individuals choose seasonal home ranges that minimize the risks to their own survival. We hypothesize that by moving to a different range during summer, migrants may have been able to increase their survival over what it might have been if they had remained year-round on their winter ranges of low quality. Migrants may have been able to compensate for home ranges of lower quality by increasing home range size in winter; this expansion would likely result in nearly equivalent survival rates for both migrants and residents until environmental conditions allow movement to summer ranges. An alternative explanation is that winter conditions experienced by deer during our study were sufficiently mild as to not affect the survival rate of individuals using winter ranges of relatively lower quality (DelGiudice et al. 2002).

Our survival estimates suggest that a winter home range of relatively low quality, as indexed by size of home ranges, did not affect survival negatively. Further study is needed to determine if this pattern is consistent across a range of winter severity, and if the trade-offs or benefits associated with migration change with environmental conditions. Our results are also consistent with the hypothesis that over time survival between residents and migrants in a partially migratory population should be equivalent (Lack 1968). A major theme in the study of migration across taxa investigates why individuals decide to migrate or remain resident. Our results suggest that density-dependent competition may play a leading role in this decision-making process, and that home range quality may influence the decision of individuals to migrate in partially migratory populations.

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LITERATURE CITED

- AVGAR, T., G. STREET, AND J. M. FRYXELL. 2014. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 92:481–490.
- BALL, J. P., C. NORDENGREN, AND K. WALLIN. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* 7:39–47.
- BISHOP, C. J., G. C. WHITE, D. J. FREDDY, B. E. WATKINS, AND T. R. STEPHENSON. 2009. Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172:1–28.
- BOYCE, M. S. 1989. *The Jackson elk herd: intensive wildlife management in North America*. Cambridge University Press, Cambridge, New York.
- BOYCE, M. S., P. R. VERNIER, S. E. NIELSON, AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- BRINKMAN, T. J., R. A. MADDOX, E. S. WILLIAMS, M. W. MILLER, P. GAMBETTI, AND L. B. SCHONBERGER. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *Journal of Wildlife Management* 69:1099–1111.
- BROWN, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. *Journal of Wildlife Management* 56:246–253.
- BUNNEFELD, N., ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- CAGNACCI, F., 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.
- CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- CHAPMAN, B., B. C. BRONMARK, J. A. NILSSON, AND L. A. HANSSON. 2011. The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- CLOVER, M. R. 1956. Single gate deer trap. *California Fish and Game* 42:199–201.
- CRAWFORD, H. S., AND R. L. MARCHINTON. 1989. A habitat suitability index for white-tailed deer in the Piedmont. *Southern Journal of Applied Forestry* 13:12–16.
- CURTIS, S. M. 2015. mcmcplots: create plots from MCMC output. R package version 0.4.2. <https://CRAN.R-project.org/package=mcmcplots>. Accessed 3 September 2013.
- DE LEENHEER, P., A. MOHAPATRA, H. A. OHMS, D. A. LYTLE, AND J. M. CUSHING. 2017. The puzzle of partial migration: adaptive dynamics and evolutionary game theory perspectives. *Journal of Theoretical Biology* 412:172–185.
- DELGIUDICE, G. D., M. R. RIGGS, P. JOLY, AND W. PAN. 2002. Winter severity, survival, and cause specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* 66:698–717.
- DEYOUNG, C. A. 2011. Population dynamics. Pp. 147–180 in *Biology and management of white-tailed deer* (D. G. Hewitt, ed.). CRC Press, Boca Raton, Florida.
- DHONDT, A. A. 2010. Effects of competition on great and blue tit reproduction: intensity and importance in relation to habitat quality. *The Journal of Animal Ecology* 79:257–265.
- ESRI. 2010. ArcMap GIS. Ver. 10.0. Environmental System Research Institute, Inc., Redlands, California.
- FRYXELL, J. M., ET AL. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Science* 105:19114–19119.
- FIEBERG, J. D., W. KUEHN, AND G. D. DELGIUDICE. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. *Journal of Mammalogy* 89:1529–1539.
- GAILLARD, J. M., M. FESTA-BIANCHET, AND N. G. YOCOZO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- GAUDRY, W., ET AL. 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an alpine population. *Journal of Mammalogy* 96:502–510.
- GAUTHREUX, S. A. 1982. The ecology and evolution of avian migration systems. Pp. 93–168 in *Avian biology*, volume VI (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, New York.
- GROVENBURG, T. W., J. A. JENKS, R. W. KLAVER, C. C. SWANSON, C. N. JACQUES, AND D. TODEY. 2009. Seasonal movements and home ranges of white-tailed deer in north-central South Dakota. *Canadian Journal of Zoology* 87:876–885.
- GROVENBURG, T. W., ET AL. 2011. Influence of landscape characteristics on migration strategies of white-tailed deer. *Journal of Mammalogy* 92:534–543.
- GUYON, I. 1997. A scaling law for the validation-set training-set ratio. *AT & T Bell Laboratories* 80:1–11.
- HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- HEBBLEWHITE, M., AND E. H. MERRILL. 2007. Multi-scale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:377–387.
- HEBBLEWHITE, M., E. H. MERRILL, AND G. McDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.
- HEFFELFINGER, J. R. 2011. Taxonomy, evolutionary history, and distribution. Pp. 3–42 in *Biology and management of white-tailed deer* (D. G. Hewitt, ed.). CRC Press, Boca Raton, Florida.
- HEWITT, D. G. 2011. Nutrition. Pp. 75–106 in *Biology and management of white-tailed deer* (D. G. Hewitt, ed.). CRC Press, Boca Raton, Florida.
- JOHNSON, M. D. 2007. Measuring habitat quality: a review. *The Condor* 109:489–504.
- KAITALA, A., V. KAITALA, AND P. LUNDBERG. 1993. A theory of partial migration. *American Naturalist* 142:59–81.
- KELLNER, K. 2016. jagsUI: a wrapper around ‘rjags’ to streamline ‘JAGS’ analyses. R package version 1.4.4. <https://CRAN.R-project.org/package=jagsUI>. Accessed 20 September 2014.
- KÉRY, M., AND M. SCHAUB. 2012. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press, Oxford, United Kingdom.
- LACK, D. 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford, United Kingdom.
- LACK, D. 1968. Bird migration and natural selection. *Oikos* 19:1–9.
- LANDFIRE. 2014. Existing vegetation type layer. LANDFIRE 1.2.0. U.S. Department of the Interior, Geological Survey. <http://landfire.cr.usgs.gov/viewer/>. Accessed 5 January 2014.
- LUNDBERG, P. 1987. Partial bird migration and evolutionarily stable strategies. *Journal of Theoretical Biology* 125:351–360.
- LUNDBERG, P. 1988. The evolution of partial migration in birds. *Trends in Ecology & Evolution* 3:172–175.
- LUNDBERG, P. 2013. On the evolutionary stability of partial migration. *Journal of Theoretical Biology* 321:36–39.
- McLOUGHLIN, P. D., AND S. H. FERGUSON. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience* 7:123–130.

- McLOUGHLIN, P. D., S. H. FERGUSON, AND F. MESSIER. 2000. Interspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* 14:39–60.
- MIRANDA, B. F., AND W. F. PORTER. 2003. Statewide habitat assessment for white-tailed deer in Arkansas using satellite imagery. *Wildlife Society Bulletin* 31:715–726.
- MITCHELL, M. S., AND M. HEBBLEWHITE. 2012. Carnivore habitat ecology: integrating theory and application. Pp. 218–255 in *Carnivore ecology and conservation: a handbook of techniques* (L. Boitani and R. A. Powell, eds.). Oxford University Press, Oxford, United Kingdom.
- MITCHELL, M. S., AND R. A. POWELL. 2007. Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behaviour* 74:219–230.
- MYSTERUD, A. 2000. Diet overlap among ruminants in fennoscandia. *Oecologia* 124:130–137.
- MYSTERUD, A. L., E. LOE, B. ZIMMERMANN, R. BISCHOF, V. VEIBERG, AND E. MEISINGSET. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? *Oikos* 120:1817–1825.
- NAMS, V. O. 2006. *Locate III user's guide*. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.
- NATHAN, R., ET AL. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Science* 105:19052–19059.
- NELSON, M. E. 1993. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. *Journal of Mammalogy* 74:316–322.
- NELSON, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Canadian Journal of Zoology* 73:1069–1076.
- NELSON, M. E. 1998. Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology* 76:426–432.
- NELSON, M. E., AND L. D. MECH. 1992. Dispersal in female white-tailed deer. *Journal of Mammalogy* 73:891–894.
- NELSON, M. E., L. D. MECH, AND P. F. FRAME. 2004. Tracking of white-tailed deer migration by global positioning system. *Journal of Mammalogy* 85:505–510.
- NICHOLSON, M. C., R. T. BOWYER, AND J. G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammalogy* 78:483–504.
- NIXON, C. M., ET AL. 2008. Migration behavior among female white-tailed deer in central and northern Illinois. *American Midland Naturalist* 160:178–190.
- OFFICE OF WASHINGTON STATE CLIMATOLOGIST (OWSC). 2012. OWSC home page. <http://www.climate.washington.edu>. Accessed 22 March 2012.
- OWEN-SMITH, N., J. M. FRYXELL, AND E. H. MERRILL. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 365:2267–2278.
- PAC, D. F., R. J. MACKIE, AND H. E. JORGENSEN. 1991. Mule deer population organization, behavior, and dynamics in a northern Rocky Mountain environment. Montana Department of Fish, Wildlife, and Parks, Federal Aid in Wildlife Restoration, Job Compliance Report, Project W-120-R-7-18.
- PETTORELLI, N., J. M. GAILLARD, P. DUNCAN, D. MAILLARD, G. VAN LAERE, AND D. DELORME. 2003. Age and density modify the effects of habitat quality on survival and movements of Roe deer. *Ecology* 84:3307–3316.
- PLUMMER, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vienna, Austria, 20–22 March 2003.
- PLUMMER, M. 2016. rjags: Bayesian graphical models using MCMC. R package version 4-6. <https://CRAN.R-project.org/package=rjags>. Accessed 3 September 2013.
- PLUMMER, M., N. BEST, K. COWLES, AND K. VINES. 2006. CODA: convergence diagnosis and output analysis for MCMC. *R News* 6:7–11.
- R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/. Accessed 10 December 2013.
- ROTHLEY, K. D. 2001. Manipulative, multi-standard test of a white-tailed deer habitat suitability model. *Journal of Wildlife Management* 65:953–963.
- SABINE, D. L., S. F. MORRISON, H. A. WHITLAW, W. B. BALLARD, G. J. FORBES, AND J. BOWMAN. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *Journal of Wildlife Management* 66:718–728.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13:195–216.
- SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- SINGH, N. J., L. BORGER, H. DETTKI, N. BUNNEFELD, AND G. ERICSSON. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications* 22:2007–2020.
- SPIEGELHALTER, D. J., N. G. BEST, B. P. CARLIN, AND A. VAN DER LINDE. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society* 64:583–639.
- STEWART, K. M., R. T. BOWYER, AND P. J. WEISBURG. 2011. Spatial use of landscapes. Pp. 181–218 in *Biology and management of white-tailed deer* (D. G. Hewitt, ed.). CRC Press, Boca Raton, Florida.
- SU, Y., AND M. YAJIMA. 2015. R2jags: using R to run 'JAGS'. R package version 0.5-7. <https://CRAN.R-project.org/package=R2jags>. Accessed 3 September 2013.
- TAYLOR, C. M., AND D. R. NORRIS. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters* 3:280–283.
- VAN DEELEN, T. R., H. CAMPA, III, M. HAMADY, AND J. B. HAUFLE. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *Journal of Wildlife Management* 62:205–213.
- VERME, L. J. 1973. Movements of white-tailed deer in upper Michigan. *Journal of Wildlife Management* 37:545–552.
- WASHINGTON DEPARTMENT OF FISH AND WILDLIFE. 2010. Washington State Deer Management Plan: white-tailed deer. Wildlife Program, Washington Department of Fish and Wildlife, Olympia.
- WHITE, K. S., N. L. BARTEN, S. CROUSE, AND J. CROUSE. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology* 95:225–237.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

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