Habitat Quality Influences Migratory Strategy of Female White-Tailed Deer

Charles R. Henderson Jr.
University of Montana - Missoula

Follow this and additional works at: https://scholarworks.umt.edu/etd

Part of the Behavior and Ethology Commons, Population Biology Commons, Terrestrial and Aquatic Ecology Commons, and the Zoology Commons

Let us know how access to this document benefits you.

Recommended Citation
https://scholarworks.umt.edu/etd/4368

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.
HABITAT QUALITY INFLUENCES MIGRATORY STRATEGY OF FEMALE WHITE-TAILED DEER

By

CHARLES RAYMOND HENDERSON JR.

B. A., University of Tennessee, Knoxville, Tennessee, 1998

Thesis

presented in partial fulfillment of the requirements for the degree of

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

December 2014

Approved by:

Sandy Ross, Dean of The Graduate School
Graduate School

Dr. Michael S. Mitchell, Chair
Montana Cooperative Wildlife Research Unit

Dr. Paul M. Lukacs
Wildlife Biology

Dr. L. Scott Mills
Wildlife Biology

Woodrow L. Myers
Washington Department of Fish and Wildlife
Abstract Title
Habitat quality influences migratory strategy of female white-tailed deer

Chairperson: Dr. Michael S. Mitchell

Partial migration is a life history strategy that is common for ungulate species living in seasonal environments. One factor that influences the decision to migrate by ungulates is access to high quality habitat. We evaluated the influence of access to winter habitat of high quality on the probability of an individual migrating, the differences in seasonal habitat use between and within migratory and resident classes of deer, and the effects of this decision on the survival of female white-tailed deer. We hypothesized that deer with home ranges of relatively low quality in winter would have a relatively high probability of migrating, the quality of home range in summer would be approximately equal as migrants moved to relatively higher quality home ranges, survival of migrants in winter would be lower than residents due to home ranges of lower quality, and survival would be comparable in summer between migrants and residents. We radio-collared 67 female white-tailed deer (Odocoileus virginianus) in 2012 and 2013 at 7 capture sites within the study area. The odds of being a migrant increased by 3.1 per 1-unit increase in home range size and decreased by 0.29 per 1-unit increase in the proportion of cropland within home range in winter. The habitat with the highest probability of use in winter for residents was pasture (1.00, SD = 0.01) and for migrants was riparian (0.73, SD = 0.39). In summer both groups had the highest probability of using pasture (resident = 0.96, SD = 0.15; migrant = 0.99, SD = 0.08). We integrated the migration probability and survival models to estimate annual and seasonal survival rates of migrants and residents. We found little difference between the annual and seasonal rates of survival. Annual survival rates for migrants and residents were 0.87 (SD = 0.06) and 0.83 (SD = 0.07), respectively. Our results indicate that access to habitat of high quality may be a strong influence on a female white-tailed deer’s decision to migrate. We suggest the presence of partial migration in a population may be a response to competition for high quality habitat.
Migration is a life history strategy that occurs in a wide variety of taxa and encompasses a behavioral continuum from resident to migrant, influenced by changing ecological conditions (Cagnacci et al. 2011). In environments that are spatially and temporally variable, the decision to migrate has been shown to have both positive and negative influences on the components of fitness, survival and reproduction (Nicholson et al. 1997, Hebblewhite and Merrill 2008). 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.

Partial migration occurs when only a portion of the population migrates (Lundberg 1988, Cagnacci et al. 2011). Animals with high quality seasonal home ranges are not as likely to migrate, whereas those with relatively poor seasonal home ranges are more likely to migrate (Gauthreaux 1982). Thus, partial migration is a behavioral strategy that allows migrants to be competitive with animals that do not migrate; vital rates of migrants and residents should therefore be approximately equal over time for both behaviors to persist in a population (Lack 1968). Partial migration has been shown to be an individually-based evolutionary solution and density dependent (Lundberg 1988, 2013; Kaitala et al. 1993). Its magnitude within a population is influenced by the amount of competition between residents and migrants.
Partial migration from summer to winter ranges has been documented in most northern cervids, including white-tailed deer (Sabine et al. 2002, Nixon et al. 2008, Grovenburg et al. 2011), mule deer (*O. hemionus*; Brown 1992, Nicholson et al. 1997), moose (*Alces alces*; Ball et al. 2001, White et al. 2014), and elk/red deer (*Cervus elaphus*; Boyce 1989, Mysterud et al. 2011). Within this group white-tailed deer inhabit the broadest geographic range (Demarais et al. 2000, Heffelfinger 2011) and exhibit behaviors across the continuum of migratory strategies (Grovenburg et al. 2011, DeYoung and Miller 2011). This permits the investigation of the fitness outcomes resulting from different choices in migration strategy among deer that experience similar environmental conditions.

Multiple studies have investigated migration in white-tailed deer, with the majority focusing primarily on factors that influence timing of migration (Nelson 1995, Brinkman et al. 2005, Grovenburg et al. 2009). Few studies have investigated factors influencing the decision of an individual to migrate. Experiences as a juvenile have been suggested as one influence on the migratory strategy individuals adopt as adults (Pac et al. 1991, Nelson 1998). Juvenile experience, however, does not explain the common switching between migratory strategies observed in populations of white-tailed deer (Nelson 1998). Fieburg et al. (2008) demonstrated that the probability that an individual deer would be observed switching migration strategies was positively related to the number of years the individual was monitored. Grovenburg et al. (2011) evaluated how attributes of forest patches occupied by white-tailed deer (e.g., patch density, size, and shape) influenced the likelihood that an individual migrates. We expanded the scope of
our investigation to include not only important habitat attributes but, the effects of habitat quality on the choice of migration strategy.

Hall et al. (1997) defined habitat as the set of specific resources and conditions that allow an individual, species, or population to survive and reproduce. Intensity of use is often used as an indicator of fitness associated with habitat (Boyce and McDonald 1999), such that high probability of use (i.e., preference) reflects high survival or reproduction. High quality habitat for female white-tailed deer varies seasonally. In the northwestern portion of their range, the diet of white-tailed deer during winter consists of browse (74%), forbs (9%), grass (9%), and crops (6%; Hewitt 2011). Accordingly, white-tailed deer should prefer riparian areas during winter because these cover types contain large amounts of browse species. Another important component of winter habitat is closed canopy forest, which provides thermal protection, reduces snow depth, and enables individuals to conserve energy (Moen 1976, Pauley et al. 1993). The diet of white-tailed deer in summer is made up of browse (45%), forbs (34%), crops (13%), and grass (5%; Hewitt 2011), suggesting riparian areas, grasslands and pasture, and crop land will be preferred in summer. Riparian areas and pasture also provide hiding cover for fawns and should be preferred by female deer during the summer. According to the competitive release hypothesis (Gauthreaux 1982) we expected quality of home ranges in winter to influence an individual’s choice of migration strategy, with quality of summer ranges representing the outcome of that choice. We defined quality of home ranges by the proportion of preferred landcover types they contain. Further, Mitchell and Powell (2007) showed that home ranges of low quality should be larger than those of high
quality for a population of animals living on a heterogeneous landscape. We therefore also used relative size of home ranges as an index of habitat quality.

We evaluated the survival rates associated with migrants and residents for 2 reasons. First, the demographic rate of survival can be used to assess habitat quality (Hall et al. 1997). For example, the competitive release hypothesis states that residents should use higher quality habitat relative to migrants. A comparison of survival rates of the different migration strategies would assist in identifying habitats of relatively high and low quality and increase our understanding of how habitat quality influences an individual’s decision to migrate. Second, the survival rate associated with a particular strategy should account for its prevalence and continued presence in a population (Alves et al. 2013).

We investigated how habitat quality influences the decision of adult female white-tailed deer to migrate. We focused on adult females because their fitness has been shown to have the greatest influence on deer demography (Eberhardt 2002, Merrill et al. 2003). Our objectives were to predict migration strategy based on the quality of home range in winter, to evaluate differences in seasonal habitat use between and within migratory and resident classes of deer, and to quantify the effects of this decision on the survival of female white-tailed deer. We hypothesized that deer with large (i.e. low quality) home ranges with little agricultural land would have a higher probability of migrating than those with small home ranges containing relatively large amounts of agricultural land. We hypothesized that quality of summer home ranges for migrants and residents would be approximately equal because intraspecific competition should decrease when availability of high quality habitat increases and population density decreases. We
hypothesized that migrants with winter ranges of low quality would have a lower survival rate than residents with winter ranges of high quality. Finally, we hypothesized that summer survival of migrants would approximate that of residents because of the comparable quality of their summer ranges.

**STUDY AREA**

Our study area included 2 game management units (GMU), GMU 117 and GMU 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. The mean annual precipitation was 45.6 cm. Average temperatures for winter and summer were -1.7°C and 19.4°C, respectively (OWSC 2012). Land cover and ownership in the study area consisted of 57.6% privately owned land, 25.6% U.S. Forest Service, and the remaining 16.8% was split between other federal, state, and tribal agencies (WDFW 2010). The dominate land cover in the study area 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 split between cultivated crops, wetlands, urban/rural development, and broadleaf forest (WDFW 2010).
METHODS

Capture and Handling

We captured 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 weighed, conducted a physical examination, and took fecal samples from each individual. We placed numbered ear tags (Y-Tex Corporation, Cody, WY) 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 determined age in 1 of 3 categories (adult, yearling, fawn) based on tooth wear and replacement (Severinghaus 1949). We outfitted adult female deer (age ≥ 2.5 years old) with either GPS or VHF radio collars (Advanced Telemetry Systems, Inc., Isanti, MN). We equipped yearling females (age 1.5-2.5 years old) with VHF radio collars. We equipped fawns (<1.5 years old) with VHF ear tags. 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 (Gannon et al. 2007).

Migratory Status

We recorded locations for GPS-collared deer every 4 hours starting at 00:00 on even numbered days and 01:00 on odd numbered days from January 2012 to January 2014. We also gathered hourly locations between 15 November 2013 and 1 January 2014 to examine fall migration routes. We located deer with VHF collars from the ground bi-weekly and by fixed-wing aircraft 3-4 times annually depending upon resources and favorable flying conditions.
We used net squared displacement (NSD) between sequential locations to define migrant and resident deer (Bunnefeld et al. 2011, Singh et al. 2012). We calculated NSD in the R (R Version 3.0.2, www.r-project.org, accessed 10 Dec 2013) package adehabitatLT (Calenge 2006, www.r-project.org, accessed 5 April 2013) 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 non-overlapping ranges (Ball et al. 2001). We assigned deer to migrant or resident categories for analysis based on a visual inspection of NSD graphs and seasonal home ranges generated from GPS location data (Mysterud et al. 2011). Female white-tailed deer are less likely to disperse (Nelson 1993, DeYoung 2011) and females that disperse often continue to use their traditional winter range (Nelson and Mech 1992); consequently, we counted any deer observed moving to a non-overlapping home range a single time as a migrant (Fieberg et al. 2008).

**Estimating Probability of Migration**

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 and GPS locations. We defined home ranges in winter from the first 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 mid-point 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 collared deer using GPS locations using a 95% fixed kernel (Worton 1989) contour estimated in R package adehabitatHR (Calenge 2006, www.r-project.org, accessed 1 Feb 2014). We used the reference bandwidth \((h)\) as the smoothing parameter.

We determined the composition of winter home range using remotely sensed data. We obtained land cover data from Landfire 1.2.0 (Landfire 1.2.0, www.landfire.gov, accessed 5 Jan 2014). We consolidated Landfire categories into 12 habitat classes based on previous studies (Grovenburg et al. 2011, Stewart et al. 2011) that used similar landscape characteristics to assess habitat selection by white-tailed deer. We used ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) to calculate the proportion of each habitat class in each home range. We constructed 10 a priori models to estimate the probability of migrating using

\[
Pr(mig) = \beta_0 + \beta_1 WRS + \beta_2 CT,
\]

where \(mig\) is the probability of migrating, \(WRS\) is the size of home range in winter, and \(CT\) is the proportion of a land cover type within the home range. Land cover types included were: open and closed canopy forest, shrub lands, grassland, crop lands, pasture, and riparian.

**Estimating Probability of Use**

We compared proportions of our 12 habitat classes within observed home ranges to paired potentially available home ranges to estimate relative probabilities of habitat use. To estimate potentially available home ranges, we placed multiple ring buffers in 5 km intervals out to 45-km (the furthest migration we observed) around the capture location for each collared deer. For each observed home range, we randomly placed a
potentially available home range in the same buffer as the observed home range. We defined potentially available home ranges as circles with an area equal to the mean size of all observed home ranges. We calculated the proportion of each land cover type in all home ranges. We used land cover types whose estimate of probability of use had less than 10% of posterior distribution overlapping zero to construct models to estimate the relative probability of use by season.

**Survival Estimation**

We created annual encounter histories for each collared deer with a known migration strategy to estimate annual and seasonal survival rates. Individuals monitored for longer than one year contributed an encounter history for each year monitored. We created 4 a priori models to estimate survival using

$$\Pr(S) = \beta_0 + \beta_1 MS + \beta_2 seas,$$

where $S$ is the probability of survival, $MS$ is the migration strategy, and $seas$ is the season (winter or summer). We performed a joint analysis by integrating the top models from the estimation of migration probability set and the survival model set to estimate the annual and seasonal survival for migrants and residents.

**Model Analysis**

We employed a Bayesian statistical framework to conduct analysis of all of our models. We used JAGS 3.4.0 (JAGS 3.4.0, [www.mcmc-jags.sourceforge.net](http://www.mcmc-jags.sourceforge.net), accessed 3 Sept 2013), R package R2jags (Su and Yajima 2013, [www.r-project.org](http://www.r-project.org), accessed 3 Sept 2013), R package rjags (Plummer 2013, [www.r-project.org](http://www.r-project.org), accessed 3 Sept 2013) and R package jagsUI (Kellner 2014, github.com/kenkellner/jagsUI, accessed 20 Sept 2014). We standardized the size of home ranges and land cover variables to facilitate analysis.
within the JAGS program. We incorporated them into the migration prediction model using a logit link function (Kéry and Schaub 2012). We used proportion of land cover types within a home range to estimate a relative probability of use using a model with 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 2012, www.r-project.org, accessed 3 Sept 2013) and the Gelman-Rubin diagnostic test in R package coda (Gelman and Rubin 1992, Plummer et al. 2006, www.r-project.org, accessed 3 Sept 2013, Brown and Collopy 2012) and R package jagsUI. We ran models for 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). We considered models within 5 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 at predicting migration strategy by using k-fold cross validation (Boyce et al. 2002).

RESULTS

We captured deer at 7 locations within the study area and radio-collared 95 during January, February, and March of 2012 (n = 40) and 2013 (n =55) including 41 adults (37 female), 23 yearlings (20 female), and 31 fawns (12 female). We fitted deer with 37 GPS collars (21 adults, 16 yearlings), 20 VHF collars (16 adults, 4 yearlings), and 36 VHF ear tags (fawns). We used GPS locations to calculate 113 observed home ranges for winter
2011-2012 (n = 10), summer 2012 (n = 10), fall 2012 (n = 8), winter 2012-2013 (n = 24), summer 2013 (n = 23), fall 2013 (n = 21), 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 second year), and fall 2013 (n = 8, 4 of which were deer observed for a second year). No collared deer observed for >1 year switched migratory strategies.

**Estimating Probability of Migration**

We estimated the probability of migration from 74 observations of annual movement that included both migrants (n = 44) and residents (n = 30). We constructed the 74 observations of annual movement from 42 individual deer; deer monitored for more than one year contributed more than one observation.

In winter, the mean size of observed home ranges of migrants ($\bar{x} = 330.57$ ha, range = 52.61 - 1160.89 ha) was larger than for residents ($\bar{x} = 211.07$ ha, range = 65.99 - 638.87 ha). Mean size of observed home range in summer for migrants ($\bar{x} = 216.97$ ha, range = 47.69 - 1568.08 ha) was larger than for residents ($\bar{x} = 114.36$ ha, range = 41.43 - 221.21 ha). The size of potentially available home ranges used for comparison was 242 ha.

The size of home ranges in winter were positively associated with the probability of migration, with the odds of migration increasing by 3.11 (95% CRI = 0.97 – 14.54) for each unit increase in standardized home range size ($\bar{x} = 301.15$, SD = 288.05). The proportion of crop land in a winter home range was negatively associated with the probability of migration, with the odds of migration decreasing by 0.29 (95% CRI = 0.10 – 0.47) for each unit increase in the proportion of crop land.
− 0.69) for each unit increase in the standardized proportion of crop land (\( \bar{x} = 0.06, \text{SD} = 0.12 \)).

**Relative Probability of Use**

The top models for estimating the relative probability of use of habitat classes for migrants and residents varied by season. We used either the top model based on DIC score or a model within 5 DIC points of the top model. This enabled us to use the same model for both strategies to estimate relative probability of use during each season. By using the same model, we were able to compare patterns of habitat use by season between migrants and residents. The estimates of relative probability of use were low for closed canopy forest and crop land for both migrants and residents during winter. Residents had a relatively high probability of using pasture in winter, whereas migrants showed no preference. Residents and migrants both had a relatively high probability of using riparian areas during winter. Residents had high relative probabilities of using grassland, crop land, riparian areas, and pasture in summer. Migrants had relatively high probabilities of using pasture and riparian areas during summer. Migrants had relatively low probabilities of using crop land and grassland in summer (Table 2).

**Survival Estimation**

We estimated survival for 53 migrant and 39 resident female white-tailed deer. The top model for estimating survival based on DIC scores included migration strategy and season as covariates. The joint analysis of the top models from the migration probability estimation and the survival estimation resulted in an estimate of annual survival for migrants of 0.88 (SD = 0.06) and 0.83 (SD = 0.07) for residents. Posterior distributions for the 2 estimates overlapped considerably (70.5%, absolute error < 0.0001;
Figure 1) suggesting little difference in survival between the two migration strategies.

There was no difference in seasonal survival rates between strategies for all seasons (Table 3).

**DISCUSSION**

Partial migration is a life history strategy employed by white-tailed deer in the northern portion of their distribution. We sought to identify how access to winter habitat of high quality influences the decision of an individual white-tailed deer to migrate, to compare probability of using high quality habitats between migration strategies both within and between seasons, and to quantify the effect of migration on survival. To our knowledge no one has used a measure of home range quality to predict the probability of migration in white-tailed deer. Our results indicate that habitat quality of home range in winter influenced the decision of deer we observed to migrate. We found that migrants used habitat types of high quality, pasture and riparian areas, differently from residents in winter but similarly during summer. Survival rates for migrants and residents were approximately equal, both annually and seasonally, indicating that there was no fitness cost in terms of survival for the decision to migrate or having a winter range of low quality.

Our hypothesis that female white-tailed deer with relatively poor home ranges in winter are more likely to migrate to summer ranges was supported. This provides evidence that the quality of winter range directly influences an individual’s decision to migrate. We suggest that habitat quality is the basis for the decision to migrate or not and determines whether the decision will maximize an individual’s fitness. This suggests that partial migration exists within a population as a strategy that equalizes the fitness
between residents and migrants. We hypothesize that intraspecific competition, as related to access to habitat of high quality, is the mechanism that has the greatest influence on migratory decision making in female white-tailed deer.

Our hypothesis that migrant and resident female white-tailed would use habitat differently in winter was also supported. Residents had the highest probability of using pasture during winter. Conversely, migrants had the highest probability of using riparian areas and did not use pasture more or less than would be expected given its availability. The relatively large size of home ranges of migrants suggests that riparian habitat is of relatively lower quality than pasture during winter. Pasture should be a habitat of high quality in winter. It provides a variety of sources of forage (browse, forbs, grasses) and cover during the season when these resources are most limited. We suggest residents use this habitat type with a higher probability because their home ranges in winter likely contain a larger proportion of pasture and they outcompete migrants for it indirectly, through consuming resources. The limited availability of this high quality habitat, 6.6% of the total landscape and becoming less in winter due to environmental conditions, likely makes it one of the underlying reasons for the presence of partial migration in this population. We found partial support for the hypothesis that habitat use in summer would be similar between migrants and residents. Both groups shared a very high probability of using pasture and a high probability of using riparian areas in summer. The increase in the probability of using pasture by migrants supports the idea that pasture is habitat of high quality throughout the year, it is a limited resource in winter, and that deer in this population compete for it. It also suggests that migrants move to areas where they can have greater access to this resource and therefore is a proximate cause for partial
migration in this population. As expected, the relative probability of residents using crop land and grasslands increased in summer. However, migrants had a low relative probability of using crop land and grassland. We suggest this pattern of use is related to a decrease in availability of these 2 habitat types as migrants move away from the valley bottoms to areas where these habitats are less likely to occur on the landscape. The movement away from the valley bottoms likely decreases intraspecific competition by reducing population density associated with winter range.

Our hypothesis that migrant survival in winter would be lower than resident survival was not supported. This suggests that migrants are able to compensate for home ranges of relatively lower quality in winter by increasing the size of their home ranges in winter (Mitchell and Powell 2007). Another possible explanation for this result is that the winter conditions experienced during our study were too mild (Ball et al. 2001) to result in a difference of winter survival between the 2 strategies.

Our estimates for survival rates of the 2 strategies in summer supported the hypothesis that survival in summer should be equal for migrants and residents. This implies that by moving, migrants are able to increase their survival over what it might have been if they had remained on their winter ranges of low quality. These results also suggest that partial migration will result in equal fitness over time as a consequence of migrants gaining access to high quality habitat due to movement. Another survival study conducted by Nixon et al. (2008) also showed no difference in the survival rates between resident and migrant female white-tailed deer. The results from Nixon et al. (2008) and our study provide further support for Lack’s (1968) theory that migration will equalize the survival of individuals employing this strategy with that of residents eventually.
We made several assumptions whose violations could have affected the interpretation of our results. Whereas migratory behavior occurs along a continuum we classified individuals into 2 discrete categories for analysis in order to include our entire sample in the model of migration probability. If the proportion of individuals that fell outside of the resident and migrant categories (10.7%) had been larger, our ability to predict migration or residency may have been reduced. According to migration theory there should be some form of density-dependence occurring on winter range in order for partial migration to be present (Lack 1968, Taylor and Norris 2007). We did not measure density directly, but used the size of home range as a measure of habitat quality that has been shown to be density dependent (Mitchell and Powell 2007). In habitat studies estimating whether a particular habitat is preferred or not, the result is dependent on the delineation of available habitat. We addressed availability by limiting it to the furthest distance migrated by an individual in this study. We assumed this was the most appropriate scale for addressing our hypotheses comparing seasonal habitat use between and within migrant and resident classes of deer.

Our results have implications for predicting the switching of migration strategies by individuals within any partially migratory population. Nelson (1998) observed that the migration strategy of a fawn’s mother was a good indicator of its migration strategy as an adult, but 18% of the deer he observed switched strategies at some point. This would suggest that migratory decisions may be influenced by learned behavior, but this decision can also be explained as offspring making the same decisions as their mothers under similar environmental conditions. We hypothesize that as the amount of available resources change, the degree of competition for a home range of high quality should
fluctuate. We predict that a relatively large proportion of conditional migrants should remain resident when resources are abundant and competition is decreased and should migrate when resources are reduced and competition is increased. We suggest that juveniles who change migration patterns are evaluating the same quality habitats as their mothers, but they reach different conclusions about availability based upon their competitive ability.

The validity of the competitive release or dominance hypothesis for explaining migration has been documented in red deer (Mysterud et al. 2011) and moose (White et al. 2014). We propose that intraspecific competition for home ranges of high quality has the largest influence on the decision to migrate by female white-tailed deer. Our survival estimates indicate that using a home range of relatively low quality in winter did not negatively affect survival. Therefore we propose that the fitness cost of migration will be related to reproduction. We suggest that the home ranges of migrants in winter will be relatively low quality in summer and this drives the decision to migrate. We hypothesize that movement to home ranges of high quality in summer will increase reproduction relative to what it would have been had migrants remained on their winter home range. We suggest that summer ranges of high quality will increase fawn recruitment for migrants through increased survival of fawns associated with improved nutrition during lactation and post-weaning. We also propose that migration results in an improvement in the body condition of the doe during the breeding season thereby resulting in a higher probability of pregnancy and an increase in survival over winter. We conclude that the existence of partial migration in a population is likely a response to intraspecific competition for high quality habitat.
ACKNOWLEDGMENTS

Funding was provided by Washington Department of Fish and Wildlife. We thank J. Kujala for assistance in capturing and monitoring throughout the project, D. Base, the entire staff of Little Pend Oreille Wildlife Refuge, K. Eaton and the Spokane Tribe of Indians for assistance capturing and access to their property. We appreciate the contribution of the volunteers from the Inland Northwest Wildlife Council for their assistance in capturing and monitoring. We would like to thank all technicians: Erin Schlager, William Schlager, Anna Wrona, Tyler Kelly, and Mark Teynor that assisted with capture. We also thank the Stevens County Fish and Wildlife Committee for help with gaining access to private lands, all landowners especially Tony Delgado, Gary Axtell, and Kelly Singer, that allowed access to their properties during our study. We also thank M. Nordhagen for his technical assistance throughout this project. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U. S. Government.
Literature cited

Alves, J. A., T. G. Gunnarsson, D. B. Hayhow, G. F. Appleton, P. M. Potts, W. J.
Sutherland, and J. a. Gill. 2013. Costs, benefits, and fitness consequences of

Aycrigg, J. L., and W. F. Porter. 1997. Sociospatial dynamics of white-tailed deer in the

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.

Byers. 2010. Influences of wolves and high-elevation dispersion on reproductive
success of pronghorn (Antilocapra americana). Journal of Mammalogy 91:712-
721.

Belay, E. D., R. A. Maddox, E. S. Williams, M. W. Miller, P. Gambetti, and L. B.
Schonberger. 2004. Chronic wasting disease and potential transmission to
humans. Emerging Infectious Diseases 10:977-984.

Boyce, M. S. 1989. The Jackson elk herd: intensive wildlife management in North
America. Cambridge University Press, Cambridge, New York, USA.


Movement of female white-tailed deer: Effects of climate and intensive row-crop


Gannon, W.L., Sikes, R.S. & the Animal Care and Use Committee of the American Society of Mammalogists 2007: Guidelines of the American Society of


elk in a partially migratory population through forage-predation tradeoffs. Oikos 120:1860-1870.


Figures and Tables

Figure 1. Posterior distribution overlap of migrant and resident survival estimates from integrated model for female white-tailed deer in Stevens County, Washington, 2012-2014. The amount of overlap (70.5%) suggests that there is no difference between the survival estimates for migrants and residents.
Table 1. Top models by season and migration strategy for estimating the relative probability of habitat use for resident and migrant female white-tailed deer by season, Stevens County, Washington, 2012-2013.

<table>
<thead>
<tr>
<th>Season</th>
<th>Migratory Strategy</th>
<th>Model</th>
<th>DIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Migrant</td>
<td>High Canopy + Crop + Pasture + Riparian</td>
<td>100.838*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High Canopy + Crop + Pasture</td>
<td>98.975</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High Canopy + Crop</td>
<td>96.500</td>
</tr>
<tr>
<td></td>
<td>Resident</td>
<td>High Canopy + Crop + Pasture + Riparian</td>
<td>33.202*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High Canopy + Crop + Pasture</td>
<td>31.288</td>
</tr>
<tr>
<td></td>
<td></td>
<td>High Canopy + Pasture</td>
<td>34.600</td>
</tr>
<tr>
<td>Summer</td>
<td>Migrant</td>
<td>Crop + Pasture + Grass + Riparian</td>
<td>67.606*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture + Grass + Riparian</td>
<td>67.058</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture + Grass</td>
<td>68.220</td>
</tr>
<tr>
<td></td>
<td>Resident</td>
<td>Crop + Pasture + Grass + Riparian</td>
<td>67.585*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture + Grass + Riparian</td>
<td>67.056</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture + Grass</td>
<td>68.894</td>
</tr>
</tbody>
</table>

*indicates model used for final analysis

Table 2. Estimated probability of use by season and migration strategy for female white-tailed deer, Stevens County, Washington, 2012-2013.

<table>
<thead>
<tr>
<th>Season</th>
<th>Migration Strategy</th>
<th>Parameter</th>
<th>Probability of Use</th>
<th>SD</th>
<th>f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Migrant</td>
<td>High Canopy</td>
<td>0.001</td>
<td>0.016</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Crop</td>
<td>0.184</td>
<td>0.259</td>
<td>0.858</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture</td>
<td>0.537</td>
<td>0.421</td>
<td>0.539</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Riparian</td>
<td>0.735</td>
<td>0.385</td>
<td>0.742</td>
</tr>
<tr>
<td></td>
<td>Resident</td>
<td>High Canopy</td>
<td>0.016</td>
<td>0.116</td>
<td>0.985</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Crop</td>
<td>0.062</td>
<td>0.166</td>
<td>0.957</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pasture</td>
<td>1.000</td>
<td>0.008</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Riparian</td>
<td>0.693</td>
<td>0.439</td>
<td>0.693</td>
</tr>
<tr>
<td>Season</td>
<td>Migrant</td>
<td></td>
<td></td>
<td>Resident</td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>---------</td>
<td>-----------</td>
<td>-----------</td>
<td>----------</td>
<td>-----------</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>CRI</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Winter</td>
<td>0.97</td>
<td>0.02</td>
<td>0.92 - 0.99</td>
<td>0.97</td>
<td>0.02</td>
</tr>
<tr>
<td>Summer</td>
<td>0.96</td>
<td>0.03</td>
<td>0.89 - 0.99</td>
<td>0.94</td>
<td>0.04</td>
</tr>
</tbody>
</table>

- $f$ is a measure of the proportion of the posterior distribution that has the same sign (positive or negative) as the mean value of the parameter estimate.

Table 3. Seasonal survival estimates for migrant and resident female white-tailed deer in Stevens County, Washington, 2012-2014.