

University of Nevada, Reno

**Short distance migration: The role of stopovers and transitional ranges**

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## **Abstract**

Animal migration is seasonal movements between distinct ranges not used in other times of the year. Migration is a way to avoid harsh seasonal environments, obtain higher quality forage, and mitigate predation risk. Associated with migration is the use of stopovers. Stopovers are used by migratory species as locations along the migration route used to rest and replenish somatic reserves. Stopovers are well documented for long distance migrations with a focus on spring migrations, and how migrators track the phenology of spring green-up. We analyzed data from both autumn and spring migrations to see if stopover use was an important part of migratory behavior, and to identify any differences in use of stopovers between autumn and spring migrations. We captured female mule deer in summer range and fitted them with GPS iridium collars. Collars collected location data at a rate of 2 GPS location per day while a deer was in seasonal range. Once migration was initiated, collars collected 1 GPS location per hour. This method gave us fine scale movement data for periods of migration. GPS data were collected for autumn and spring migrations from autumn 2015 until spring of 2018. We developed a frequency distribution of these stops and found that a 2-day stop during migration was the most frequent duration of a stop. We determined that stopover use was an important part of migration behavior by this population. We identified that stops during this short distance migration ranged from 1 to 145 days. We used snow water equivalent to determine the onset of winter. The first day with a snow water equivalent of 10 mm or more was assigned as the onset of winter. The frequency distribution had a decline at stops with a duration of 10 days. Based on the frequency distribution of stops by this population of mule deer, we conservatively labeled a stop with a duration of 1-10

days a stopover. A stop with a duration of 10 days or longer we considered to be transitional range. Stopovers and transitional ranges were used during both autumn and spring migrations. We found that stopovers were used in similar rates in all autumn and spring migrations with the exception of the spring migration of 2018 where use was significantly higher. Use of transitional range was similar for autumn and spring migrations from autumn 2015 to spring of 2016. There was significantly higher use of transitional range for the autumn migration of 2017 and spring migration of 2018. Years with onset of winter occurring later in the year positively influence the number of days spent in transitional range. Conversely, less time was spent in transitional range when the onset of winter occurred earlier in the year. Timing of snowfall did not affect the start of migration which was consistent across time of the study. When looking at the proportion of days stopped while on migration (combining stopovers and transitional range), was a significantly higher proportion during autumn migrations when compared to spring. The short distance migration used by this population of mule deer allows for flexibility in migrational behavior. We observed variation among individuals in use of stopovers and transitional ranges. We also found that the population varies its use of stopovers and transitional ranges based on the onset of winter and the first snowfall of the winter season. This information will elucidate individual variation in migratory behavior as well as, at a population level, how migratory behavior can be influenced by weather events.

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## 1. Introduction

Migration is one of the most widely observed and spectacular phenomena in the animal kingdom, and occurs among a wide range of taxa from insects to vertebrates (Berger, 2004). Migration is defined as two-way movements between distinct seasonal ranges that are not used during other times of the year (Berger, 2004; Dingle and Drake 2007). Berger (2004) described long-distance migration of terrestrial mammals to be among the most imperiled of Earth's natural phenomena. Indeed, interest in conserving migratory corridors, especially for species of large mammals, has been heightened in recent years. In February 2018, Secretary of the Interior, Zinke, released Secretarial Order 3362 aimed towards conserving migration corridors and improving habitat quality of winter range for big-game species in the west.

Migrations of terrestrial mammals may be long distance ( $\geq 50$  km), but also may be short distances that result in shifts in elevation, or may be shifts to and from discrete locations determined by resource abundance (Mysterud et al., 2007; Sawyer et al., 2016). Such migratory movements are dependent on elevational changes to help escape harsh seasonal environments or to obtain resources during winter that may not be available on snow-covered summer ranges. Holding areas or transitional range are locations along the migration route where individuals may linger from days to weeks and may or may not continue along the migratory pathway (Bertram and Rempel 1977; Loft and Bleich 2014).

Transitional range is usually located in the intermediate elevations between summer and winter ranges (Kucera 1992). During spring migrations, transitional range is used to wait for a decrease in snow depth on summer range or to track increasing plant

phenology, or “green up” on higher elevations (Bischof et al., 2012; Loft and Bleich 2014). Conversely, use of transitional range, during autumn, occurs in areas where individuals can obtain higher quality forage than available on winter range, but also can make a rapid descent in elevation to avoid harsh weather (Bertram and Rempel 1977).

Stopovers are locations along the migration path where the migrating individual stops for a short time to rest and restore somatic reserves depleted as a result of the energetic cost of movement to that point (Dingle and Drake, 2007; Sawyer and Kauffman, 2011). Use of stopover locations during migration has been identified in insects (Meitner et al., 2004; Wikelski et al., 2006), birds (Moore and Kerlinger 1987; Yong et al., 1998; van der Graaf et al., 2006), and ungulates; (Sawyer and Kauffman 2011). Among birds, energy gained while occupying stopovers is then used during the following flight (Rguibi-Idrissi et al., 2003) and also minimizes the duration of migrations (Hedenstrom and Alerstam 1998). Conversely, terrestrial mammals may vary in use of stopovers during spring versus autumn migrations. During spring, ungulates use stopover locations to await green-up at higher elevations, but use of stopovers is not believed to expedite migration (Fryxell, Wilmshurst and Sinclair 2004; Holdo et al., 2009; Monteith et al. 2011, Sawyer and Kauffmann 2011, Monteith et al., 2018; Wilmshurst et al., 1999). The “green wave hypothesis” suggests that, during spring, a migrating herbivore will synchronize migration with the phenology of plant green-up to maximize forage quality as they move up in elevation to summer range (Bischof et al., 2012; Merkle et al., 2016).

Less studied, however, has been the use of stopovers by terrestrial mammals in autumn, during which the migrator leaves summer range and undertakes the energetically

taxing movement to winter range. The amount of time spent at some stopovers likely indicates that they are important locations for resting during migration and likely offer additional benefits to the individual (Sawyer and Kauffmann 2011). For example, autumn migrations occur at a crucial time because the migrator must not overly deplete somatic reserves needed to survive the nutritional strain of winter. As a result, autumn stopovers during short-distance migrations may have a greater role in preparing individuals for overwinter survival than in replenishing somatic reserves used during a short-distance migration. Ungulates in good condition often will linger in higher elevations later into autumn than younger or poorer condition animals, and will remain on summer range until weather events push them to move down to winter range (Monteith et al., 2011). The benefit to staying at higher elevations until the onset of winter is the ability continue to exploit resources on summer range, as well as to avoid dense populations and greater competition for fewer resources on shared winter range (Mysterud 2013). Autumn stopovers sites also provide benefits, because Individuals that forage at higher elevations generally have access to higher quality forage than on winter range, and are able to move to winter range when forced by snow (Morellet et al., 2013). Perhaps autumn migrations are driven by weather events with oncoming winter or senescence of vegetation on summer ranges pushing animals to move towards winter ranges.

Advancements in telemetry technology have given us the ability to obtain movement data at increasingly finer scales. Those data provide an opportunity to study more precisely the temporal aspects of migration, including variation among individuals in timing, pathways used, and use of stopovers during migratory movements. Therefore, we are also able to obtain more precise and detailed information on migratory pathways,

as well as variation among individuals in use of migratory corridors. Additionally, we observe flexibility in movement strategies at the individual level both temporally and spatially.

What was once broadly defined as migration can now be subset into different strategies of movements including long or short-distance migrations, exploratory movements, and range shifts. In recent years, long distance migrations by mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) have been identified in areas such as Wyoming (Sawyer et al., 2009a) and Nevada (Blum et al., 2015) as well as locations and use of stopovers. There is a paucity of information, however, on short distance migrations and whether those individuals that could complete the migration in a single day, would use stopovers. Additionally, how do individuals vary in use of stopovers and migratory corridors, and does use of stopovers vary between spring and autumn migrations?

We used mule deer as our study species to better understand the variability in movements among individuals during migration. Mule deer occupy a wide range of habitats and demonstrate a continuum of behaviors, including short and long distance migrations and use of stopovers during migratory movements. Our purpose was to determine if and to what extent, mule deer exhibiting short distance migration used stopovers, and to explore variation such as timing of migration, duration of migrations and use of stopovers among individuals during migratory movements. We hypothesized that mule deer exhibiting short distance migrations would use stopovers, but use and duration of time spent at stopovers would vary among individuals. Further, we hypothesized that during autumn, migrating deer would linger in mid-elevation areas to

maximize forage availability, quality, and quantity prior to descending to winter range. Because short distance migrations could be completed in 1-2 days, we predicted that mule deer would not use stopovers to the same extent during spring because they would not need staging areas to wait for green-up part of the way through migratory movements, which has been observed in animals exhibiting long-distance migrations. Therefore, we hypothesized that mule deer exhibiting short distance migrations would be more likely to use stopover locations during autumn compared with spring, but individuals would vary in the use and duration of use of stopovers.

## **2. Methods**

### 2.1 Study Area

To test our hypotheses, we examined migratory behavior in a population of mule deer found on the western slope of the Sierra Nevada in eastern California. Mule deer comprising this population use a short distance migration, averaging 30 km, to move between upper elevation summer ranges and lower elevation winter ranges. This population described as the Pacific Deer Herd occurs on the western slope of the Sierra Nevada in El Dorado County, California (Fig. 1). Upper elevations (1500-2300 m) are used during summer (mid-April to mid-October), mid-elevations are used primarily during spring migration (March-May), autumn migrations (September-November), and lower elevations are used during winter (November-March). Mule deer in this population occupy upper elevations during the summer, during parturition and when females have dependent young. During mild winters, mule deer may linger in these upper elevations into late December dependent upon depth of snow. Summer range is primarily woodland

habitat comprised of mixed conifers, dominated by Ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*). Shrubs include mountain whitethorn (*Ceanothus cordulatus*) and buck brush (*Ceanothus cuneatus*). Average summer temperature is 13°C, with highs reaching 35°C, and average summer precipitation is 225 mm (<http://ClimateEngine.org>).

Mid-elevations, through which migrations occur, range between 1100-1500 m, and are characterized by high levels of disturbance (clearcutting or fire) that have created a fragmented landscape. Use of mid-elevation habitat by mule deer is greatest during autumn migration (mid-October through December), but deer may linger in these areas well into March during mild winters. Deer also use those mid-elevations during spring migration (mid-April to June). There have been instances of deer using mid-elevation zones during winter. Recently disturbed areas within the mid-elevations consist of low shrub canopy including deer brush (*Ceanothus integerrimus*), mountain misery (*Chamaebatia foliolosa*), and young trees in early successional stages, including thin leaf alder (*Alnus tenuifolia*) and California black oak (*Quercus kelloggii*).

The onset of winter was determined by the first day that 10 mm of snow-water equivalent was recorded by a SNOTEL location at Robbs Powerhouse within the study area. December 1<sup>st</sup> was day (NRCS SNOTEL, Robbs Powerhouse). During winter, the migratory portion of the population intersperses with resident deer at lower elevations (700 m – 900 m). Average winter temperature is 10°C, and average precipitation, which is highly seasonal, is 550 cm (<http://ClimateEngine.org>). Migratory deer remain at lower elevations from late October to late May or early June. The lower elevations are characterized by open woodlands containing blue oak (*Quercus douglasii*), manzanita

(*Arctostaphylos manzanita*), and gooseberry (*Ribes californium*). Vegetation is dense with high amounts of tree cover.

The King Fire, a high severity fire, burned 390 km<sup>2</sup> across much of the mid-elevational area during September and October of 2014. Plant succession following the fire has modified the way mule deer used the area. In the first year following the King Fire mule deer avoided the burned area (Brazeal et al., 2016). In subsequent years, however, GPS telemetry data show increased use of burned habitat, with some individuals remaining in that area throughout winter.

The Crystal Basin Recreational Area (344 km<sup>2</sup>) is located within the Eldorado National Forest and includes most of the summer range of this population. Crystal Basin has 25 developed campgrounds with over 700 campsites. There are over 2,900 km of paved and dirt roads, 5 lakes, and numerous streams within the recreational area. No other large wild ungulates are found within this study area. There is a suite of predators capable of killing mule deer occurs throughout the study area, among which are coyotes (*Canus latrans*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and mountain lions (*Puma concolor*).

## 2.2 Animal Capture and Handling

Adult female mule deer were captured ( $n = 44$ ), using chemical immobilization by free-range darting (Casady and Allen, 2013). We used a combination of Telazol (Dose range = 100 mg – 120 mg) and Xylazine (Dose range = 100 mg – 120 mg) to immobilize deer; after 60-90 minutes we reversed the xylazine with 2 cc of Tolazine (Casady and Allen, 2013).. Individuals were classified as adult, yearling (1-yr old), or juvenile. Mule



deer were fitted with Vectronic Plus Vertex Survey Iridium collars that provided GPS locations with a duty cycle of one-hour intervals during migrations and 12-hour intervals while in either summer or winter range, and VHF signals that could be monitored by handheld telemetry. Individuals were fitted with ear tags so that they could be identified beyond the battery life of the collars. All animal handling was approved by California Department of Fish and Wildlife and were in keeping with guidelines established by the American Society of Mammalogists for care and use of wild mammals in research (Sikes et al., 2016).

### 2.3 Statistical analysis

We collected GPS locations (1 location/hr) continuously during active migrations from 2015 to 2018. Mule deer migrations with time interval greater than 1 hour between consecutive GPS locations were omitted in the Brownian bridge movement models. We also removed any GPS locations with a Dilution of Precision (DOP)  $> 10$  or  $< 1$ . We used a minimum convex polygon (MCP) on all animal locations during winter and summer separately to define the study area and to identify the extent of each of those seasonal ranges (Blum et al., 2015; Saher and Schmiegelow 2005; Sawyer et al., 2009a). We then considered the onset of migration for each individual deer to occur when three consecutive GPS points from the individual collar left seasonal range without returning within the same season (Saher and Schmiegelow, 2005). Forays out of seasonal range with a return during the same season were considered exploratory movements (Pépin et al., 2008). Exploratory movements had an average duration of 4.4 days.

To determine if mule deer exhibited stopover behavior, we created a Brownian Bridge Movement Model (BBMM; Horne et al., 2007; Sawyer et al. 2009; Blum et al., 2015). We used the BBMM package in R 3.6.2 (R Core Team 2019) to estimate stopover locations for all individuals that completed an autumn migration. The BBMM uses consecutive GPS locations to estimate a utilization distribution (UD) based on the time interval between locations, the distance between locations, and the speed at which an animal traverses the distance between those locations (Horne et al., 2007), and estimates the probability of how far off the straight-line path between the locations an animal had moved (Horne et al., 2007; Sawyer et al., 2009; Blum et al., 2015). We used the top 25% quantile of the UD to estimate when movement became less directional and assumed deer remained at a stopover (Sawyer et al., 2009a; Blum et al., 2015). To delineate the ecological importance of stopovers we used a frequency distribution of the duration of migratory stops to determine the frequency of time spent at stopovers. We used the proportion of total migration days spent in transitional range, and performed a standard arcsine-squareroot transformation on those proportions to fulfill assumptions of normality (Zar 2010). We used a Z-test for proportions to compare the proportion of deer using stopovers versus transitional ranges (Zar 2010). We used a t-test to compare time spent on transitional ranges among seasons (Zar 2010). We used linear regression with days spent at transitional range as our response variable and onset of winter is the independent variable to test if onset of winter influenced the amount of time a deer would spend in transitional range.

### 3. RESULTS

We recorded 125 migratory events from 44 female mule deer. Onset and duration of migration varied among seasons and years. Generally, animals in our study began autumn migration on October 24 ( $\pm 13.9$  days [SD]) and began spring migration on April 30 ( $\pm 30.85$  days). The mean duration of autumn migrations was 23.72 ( $\pm 30.89$  SD) days ( $n=73$  migratory events) and mean spring migration duration was 16.35  $\pm$  14.40 days ( $n=52$  migratory events). The mean distance of these migrations was 31.99 ( $\pm 7.77$  SD) km.

Brownian Bridge Movement Models estimated the population level migration corridor (Fig. 2). Individual level Brownian Bridge Movement Models showed variation in migration routes and stopovers. (Fig. 3). Brownian Bridge Movement Models estimated 33 stopover locations used during autumn migration. Size of stopovers used was 0.27 ( $\pm 0.90$  SD) km<sup>2</sup>. The proportion of collared individuals using stopovers was 0.43. During autumn, deer spent 4 ( $\pm 2.18$  SD) days at stopovers. We recorded 52 spring migrations, during which we observed stopover behavior 11 times with a proportion of collared individuals using stopovers of 0.21; duration of spring stopovers was 5.39  $\pm$  3.13 days. During autumn migrations deer that used stopovers spent 0.29 ( $\pm 0.32$  SD) of migration days at stopover locations. During spring migrations deer spent 0.14 ( $\pm 0.28$  SD) of migration days at stopovers. The median frequency of time spent at stopovers was 2 days with the curve sharply dropping off at 10 days (Fig. 4). When we combined the total proportion of stopover use and transitional range by autumn and spring migrations, there was significantly higher use in autumn (Fig. 7). We observed slightly higher use of stopovers in autumn compared to spring (Fig.5) and significantly higher use of stopovers

in the spring 2018 migration compared to all other autumn and spring migrations during our study.

We observed 36 instances of individuals using transitional range during migration and ranging in duration from 11-145 days. Mean size of transitional range was  $2.528 (\pm 3.08)$  km<sup>2</sup>. Within autumn migrations we observed 24 instances of the use of transitional range (0.36 of collared individuals) with a mean duration of time spent on transitional range of  $36.24 (\pm 29.89)$  days. During autumn migrations deer spent  $0.43 (\pm 1.31 \text{ SD})$  of migration days on transitional range. During spring migrations, we observed 12 instances of use of transitional range with the mean time spent on transitional range of  $19.69 \pm 8.89$  days. During spring migrations deer spent  $0.20 (\pm 0.40)$  of days on transitional range. The highest amount of stopover use was the spring of 2018 (Fig. 5). There was no significant difference in the use of transitional range with consecutive (autumn/spring) migrations. There was significantly higher use of transitional ranges during the autumn 2017 and spring 2018 migrations. (Fig.6). The total proportion of number of days spent stopped during migrations were significantly higher during autumn ( $0.464 \pm 0.0938$ ) migrations when compared to spring ( $.034 \pm 0.091$ ) (Fig. 7).

The beginning of autumn migration for this population was October 21 ( $\pm 3.55$  days) during the course of this study regardless of the onset of winter. The onset of winter was either negative (10 mm of snow water equivalent before December 1<sup>st</sup>) or positive (10 mm of snow water equivalent after December 1<sup>st</sup>). The linear regression model showed that the onset of winter influenced the amount of migrations days spent in transitional range ( $r^2 = 0.922$ ; p-value = 0.002342; n = 24). The later the onset of winter lead to a higher proportion of migration days spent in transitional range (Fig. 8) The

mean start date of autumn migrations was October 21 ( $\pm 3.55$  days). The mean start date of spring migration was April 17 ( $\pm 12.5$  days). Regression analysis showed a significant relationship between onset of winter and proportion of time spent in transition range or stopovers.

#### **4. DISCUSSION**

Our hypothesis that this population of migratory mule deer used stopovers during their short distance migration was supported. We observed some deer completing their migration in 1-2 days with no stops that lasted longer than a few hours, but those observations were rare. Although, we observed 2 individuals that did not use stopovers while migrating either during autumn or spring, most of the deer in this study used stopovers during both seasons. A stopover is generally defined as a location used to rest and replenish energy stores, although an extended stop may be more than resting and replenishing reserves.

Studies have shown that plant senescence at mid-elevation occurs later in the year than at high or low elevations (Bucher and Romermann, 2020; Vitasse et al., 2009). Additionally, spring green-up occurs at higher elevations leading to higher forage quality in late summer (Myserud et al., 2017). Spatial use by ungulates is tied to phenological changes in quality of forage, which is a strategy to increase body mass prior to winter (Hila et al. 2022; Pettorelli et al., 2007). Mautz (1978) described the yearly fat cycle in deer, where the ability to acquire higher quality forage in autumn was important to offset the effects of limited forage availability during winter and ultimately excessive weight

loss leading to mortality in early spring. Extended stops at these mid-elevations during autumn may be strategies to maximize higher quality forage between seasonal ranges.

An extended stop during an autumn migration, however, may be a way to mitigate competition for limited resources in crowded winter ranges. Most stopovers lasted about 2 days, therefore longer duration stops may need a different definition because longer stops likely were more than just to rest and replenish lost resources. Therefore, to be conservative and based on our frequency distribution of stopovers, we classified any stop that was 10 days or fewer as a stopover. Based on the migratory behavior of this population we consider a stop ranging from 2-10 days to be a stopover and a stop with a duration of longer than 10 days to be an individual using transitional range. Our data indicate that 10 days is more than adequate time to rest and replenish lost reserves during a 30 km migration. We classified stops with a duration of 11-145 days as transitional range because those extended stops occurred in the mid-elevation transitional areas between summer and winter home ranges.

There was variation in the timing and severity of winter during this study. The winter of 2015-2016 saw the earliest onset and the lowest snowfall. Winter of 2016-2017 recorded the greatest snowfall during the study and with the onset occurring on the 30-year median. The winter of 2017-2018 was the latest onset and the amount of snow was equal to the 30-year median. The variation in timing of the onset of winter did elucidate how seasonal differences influenced migration behavior.

We observed similar use of transitional ranges in consecutive autumn and spring migrations with significantly higher use in the autumn 2017 and spring 2018 migrations. Use of transitional range was influenced by the onset of winter rather than the amount of

snowfall. A later onset of winter resulted in more time spent in these transitional ranges. A change in the timing of winter precipitation can result in a change in the phenology of forage in spring and autumn. (Xu and Si, 2019). Deer may be tracking those changes, either green-up or senescence, and adjusting their time spent in transition ranges to exploit forage resources there. Interestingly, neither the onset of winter nor the severity of winter influenced the start of migration. Throughout the study there was no significant difference in the onset of either autumn or spring migration.

Therefore, use of stops, either stopover or transitional range, during spring may be constrained by parturition, because females gave birth in summer range where and when forage quality is highest. During autumn migration, however, when there is more flexibility in the duration of migration, we observed more time spent at transitional ranges as well as more variation in the number of days spent in those locations. Likely, most mule deer in this population can complete migration in a single day. When early season storms occurred, individuals in this population could quickly retreat to lower elevations to avoid being trapped by deep snow. Because of that ability to rapidly move to lower elevations, individuals in this population did not have to complete migration as fast as possible. The entire length of the migration route is available to them within one or two days, therefore individuals likely were tracking senescence of forage as they move downslope during autumn migration. That behavior likely reduced intraspecific competition for forage on winter range, because our study population competes for resources with resident deer that live there year around. This strategy of lingering at transitional range may be effective for maximizing access to resources by avoiding winter range where forage quality is low and competition is high (Parker et al., 2009;

Courtemanch et al., 2017) leading to a more rapid decrease in somatic reserves when individuals are on winter range (Courtemanch et al., 2017; Parker et al., 2009)

Little research has been conducted on use of stopovers by ungulates during autumn migration; most documentation on use of stopovers by ungulates is during spring or by those exhibiting long-distance migration (Blum et al., 2015; Sawyer et al., 2009b; Sawyer and Kauffman, 2011). We observed substantial variation among individuals in use of stopovers, some individuals used stopovers over multiple years, while others did not use them at all. In general, females used stopovers and transitional range more frequently during autumn migrations than during spring. Use of stopovers, especially during autumn, has been well documented in the avian literature, however, and movements by mule deer in our study have many similarities in behaviors exhibited by avian species using stopovers. Chevallier et al., (2011) studied migration strategies of Black Storks (*Ciconia nigra*) migrating from West Europe and West Africa. They observed variation in individual choice in the use of stopovers; some of the migrants in their study flew non-stop to seasonal ranges during migration, while others in the same population used stopovers. When comparing potential breeders and non-breeders, Chevallier et al. (2011) observed that non-breeders used as many stopovers in autumn as they did in spring, but potential breeders used more stopovers during autumn migrations (Chevallier et al., 2011). Additionally, during autumn migrations reed warblers also had longer duration and more frequent stopovers than they showed during spring migrations (Rguibi-Idrissi et al., 2003).

Use of stopovers during migration by avian taxa has long been well studied, and only recently has stopover use by terrestrial migrants has been a focus of research.



Sawyer and Kauffman (2011) studied ecology of stopover use by terrestrial migrants, and reported, as we also observed, that migrating deer can complete the totality of their migration distance in much less time than they actually do. Instead of maximizing the speed of migration, migrating ungulates, during spring, maximized the quality of forage by tracking plant phenology as they moved along the migratory pathway (Merkle et al., 2016; Sawyer and Kauffman, 2011). Tracking plant phenology during migration has, up to now, been focused on green-up during spring migration, described as ‘surfing the green wave’ (Bischof et al., 2012). We observed that during autumn migrations, mule deer used transitional ranges at a higher rate and for longer durations than stopovers. The two longest stays at transitional range that we observed were > 140 days, and both of those instances were observed during autumn. These individuals did eventually continue to winter range for a short time before migrating back to summer range. We suggest that autumn migration and tracking forage quality ahead of plant senescence, as individuals move to lower elevation winter ranges is of equal or greater importance in some populations of mule deer and possibly other terrestrial migrants.

We observed that use of stopovers and transitional ranges during autumn minimized time spent on winter range, thus reducing intraspecific competition for resources, and appeared to result in better body condition of females earlier in spring. The ability to delay the arrival on winter range likely minimized competition with year-round resident mule deer using those locations. When occupying stopovers and transitional range during autumn migration, individuals in our study appeared to slow depletion of somatic reserves by foraging on higher elevation sites likely with higher forage quality compared to winter range. This behavior seems to help slow use of somatic

reserves through winter, and results in females on higher plane of nutrition in spring. We suggest this carry over effect of body condition for those adult females likely provided the benefit of higher fitness than those individuals occupying the defined winter range.

Few studies have elucidated the importance of behaviors associated with migration during autumn, especially among terrestrial migrants using a short-distance migration. We have shown that use of autumn stopovers and transitional range is an important strategy during migration. The flexibility of a short distance migration is likely maximized during autumn migration when females are not constrained by parturition. We have observed individuals occupy stopover locations, then be forced farther down the migration route by a weather event, only to return upslope when the weather event passed. This behavior is undoubtedly not beneficial when winter and summer ranges are separated by long distances. Nevertheless, during a short distance migration this behavior may maximize quality of forage intake and reduced competition in crowded winter ranges.

We observed high fidelity by individuals to migration strategy and to stopover locations. We observed deer using the same stopover consistently during this study. A few individuals never used stopover or transitional range during either migration. Other individuals only used stopovers or transitional ranges during either autumn or spring, but not both seasons. Some individuals lingered on transitional ranges for extended durations and tended to do so every year. Future research should include evaluating the variation and similarities in migration strategies by individuals in combination with their relatedness because those strategies likely are learned behaviors. Evaluating how use of stopovers affect recruitment also needs further study.

This study system with a short distance migration allows for diverse strategies in migration behavior. We found, at the individual level, that mule deer were relatively specialized in their migration strategy. There were deer that would use stopovers during autumn migrations and not during the spring. Some deer that used transitional ranges during autumn migrations and not during spring. At the individual level, we observed strong fidelity to a migration strategy and we did not see a switching of strategies by any individual. We would refer to these individuals as specialists in migration behavior. This population was able to alter their use of transitional range and stopovers based on the timing of onset of winter. A later the onset of winter increased the number of days spent at stopovers and transitional range. Interestingly, the amount of snow did not influence the amount of time at stops. The winter of 2016 was significantly higher snowfall than the winters of 2015 and 2017, but use of transitional range during these winters were similar. The highest use of transitional range occurred during the winter of 2016. This was not the highest snowfall recorded during this study. It was, however, the latest onset of winter beginning 49 days past December 1<sup>st</sup>. During 2015, we observed the earliest onset of winter (49 days before December 1<sup>st</sup>), and the lowest proportion of use of transitional range by migratory deer. At the population level, however, because of the multiple strategies we observed, we would define these migrators overall as generalists. At the individual level migrators within our study specialized in movement behavior and consistently used a preferred strategy. At the population level however, this study system allowed for a wide range of successful movement behaviors which can be adjusted based on seasonal variation in snowfall. Migration routes are much more than “sidewalks” that link seasonal ranges. The importance of seasonal ranges and migration corridors long has

been recognized (Loft and Bleich 2014); we suggest that characteristics of the locations at which migratory ungulates spend time during stopovers are important to further understanding the complexities of migratory behavior, particularly among ungulates. We propose that stopover and transitional ranges in addition to corridors and seasonal ranges need to be part of that conversation.

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Figure 1. Map displaying study area located on the western slope of the Sierra Nevada Mountains, El Dorado County, California, USA. Highlighted is the extent of mule deer movement by the 44 collared females in this study (2015-2018).

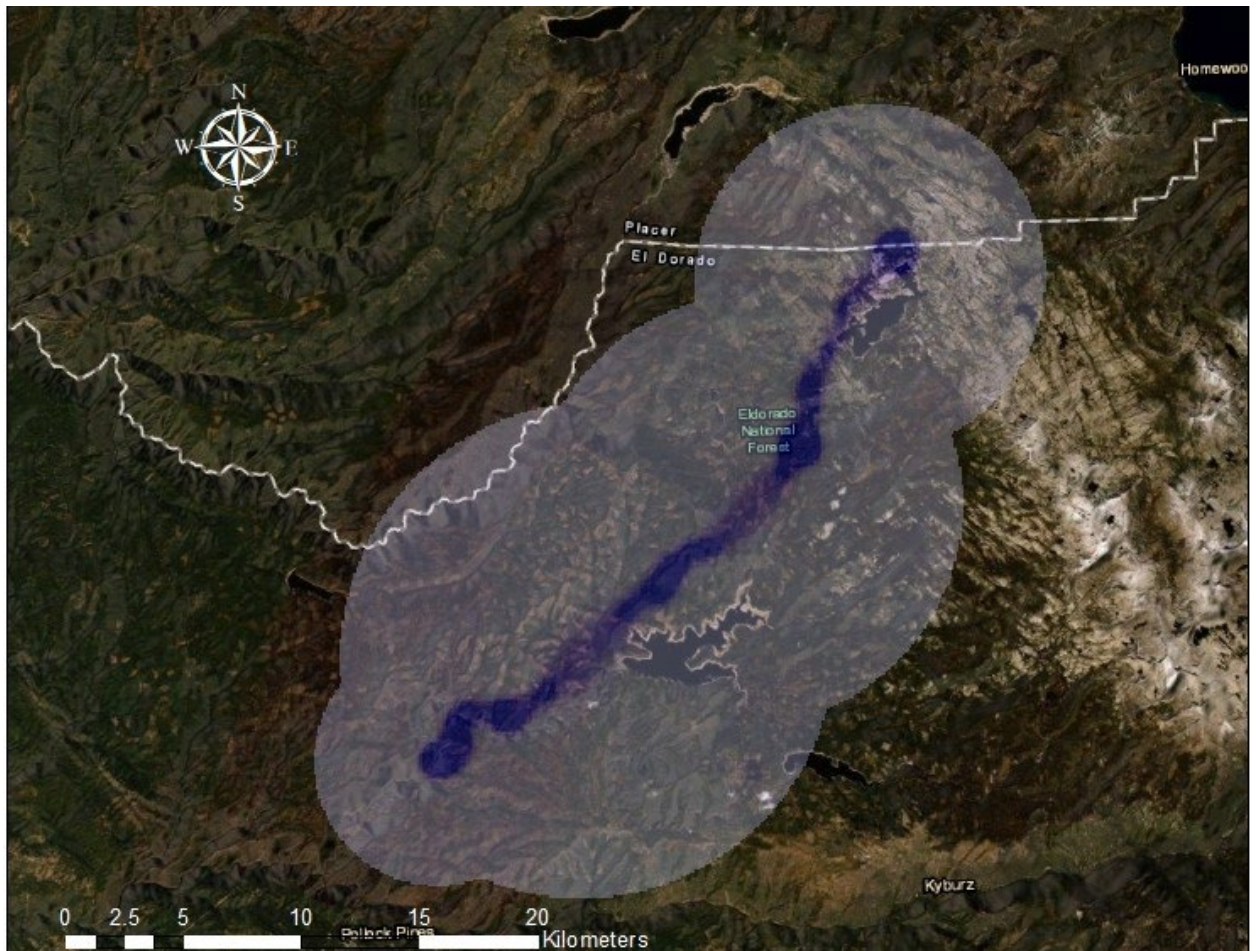


Figure 2. Map displaying the combined Brownian Bridge Movement Model of 44 collared individuals representing this population of female mule deer in the Sierra Nevada Mountains, El Dorado County, California, USA. (2015-2018).



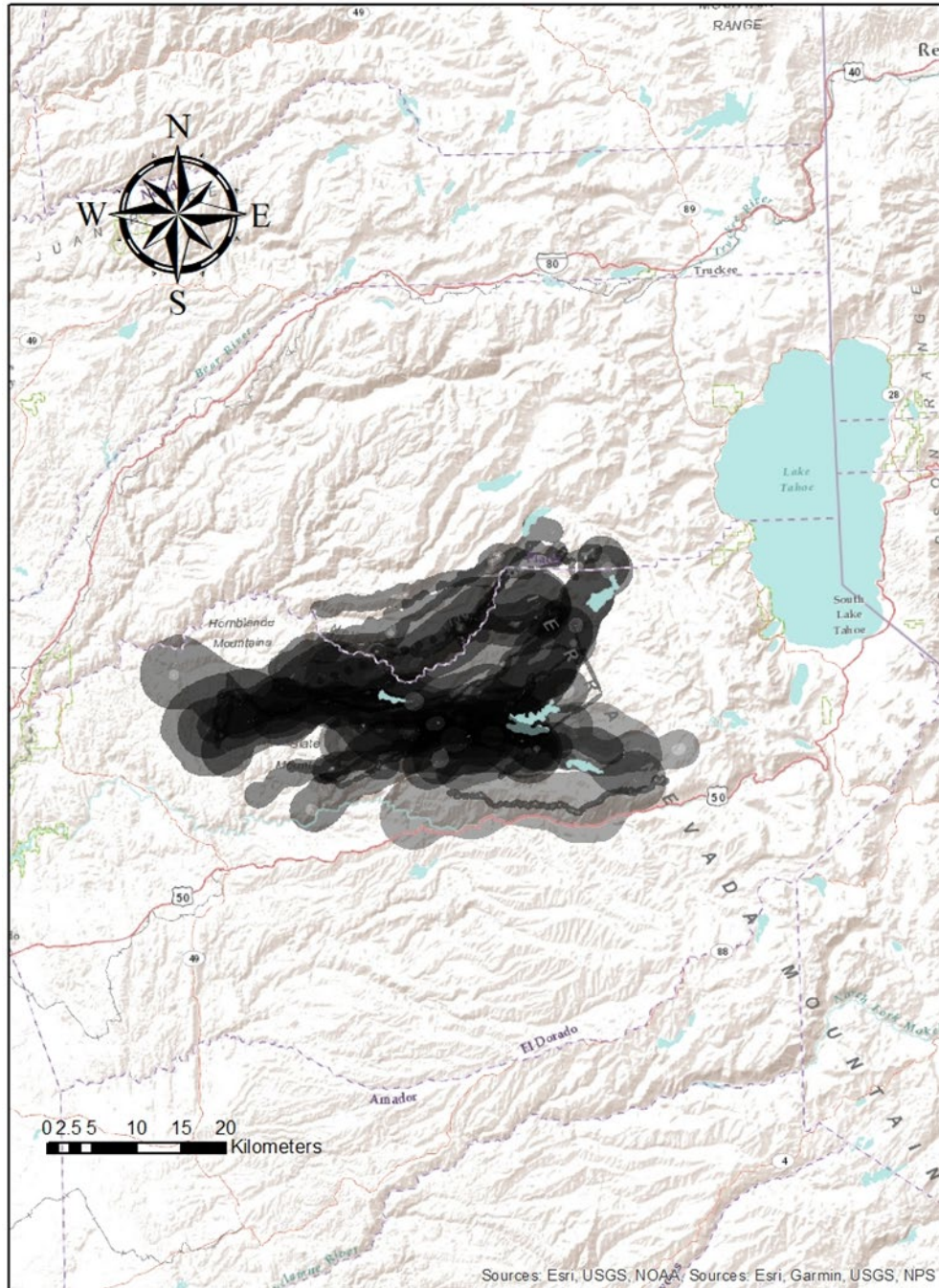


Figure 3. Individual Brownian Bridge Movement Models (BBMM) for female mule deer in the, Sierra Nevada Mountains, El Dorado County, California, USA. (2015-2018). Individual BBMMs are grayscale. Areas of overlaid BBMMs become darker. The dark area indicates the highest use by multiple female mule deer.

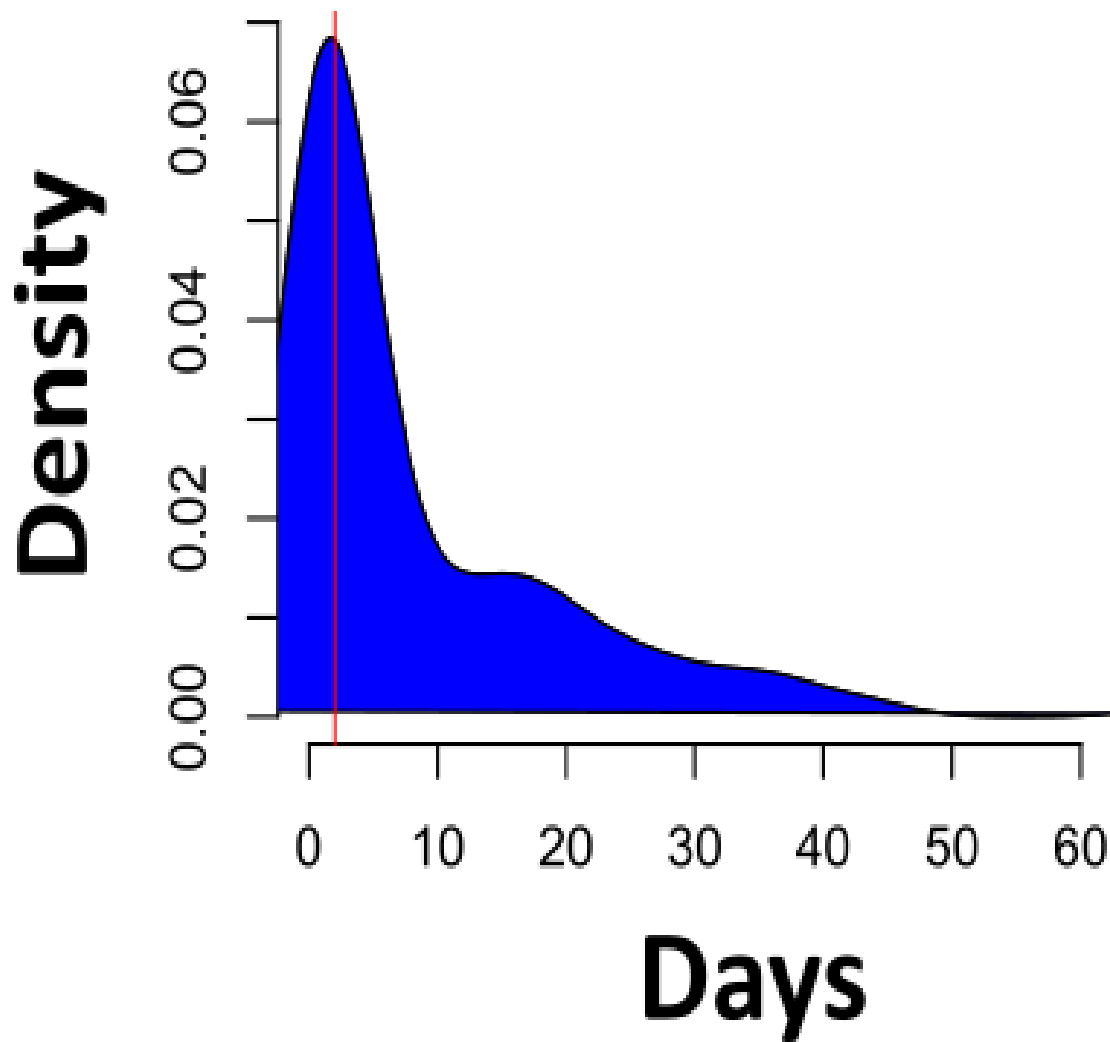


Figure 4. Frequency distribution of number of days spent stopped during migration. For clarity, the x-axis is limited to 60 days even though there were stops lasting up to 145 days. The vertical line indicates the mean duration (2 days) of a stop. These data were obtained from 44 female mule deer in the, Sierra Nevada Mountains, El Dorado County, California, USA. (2015-2018).

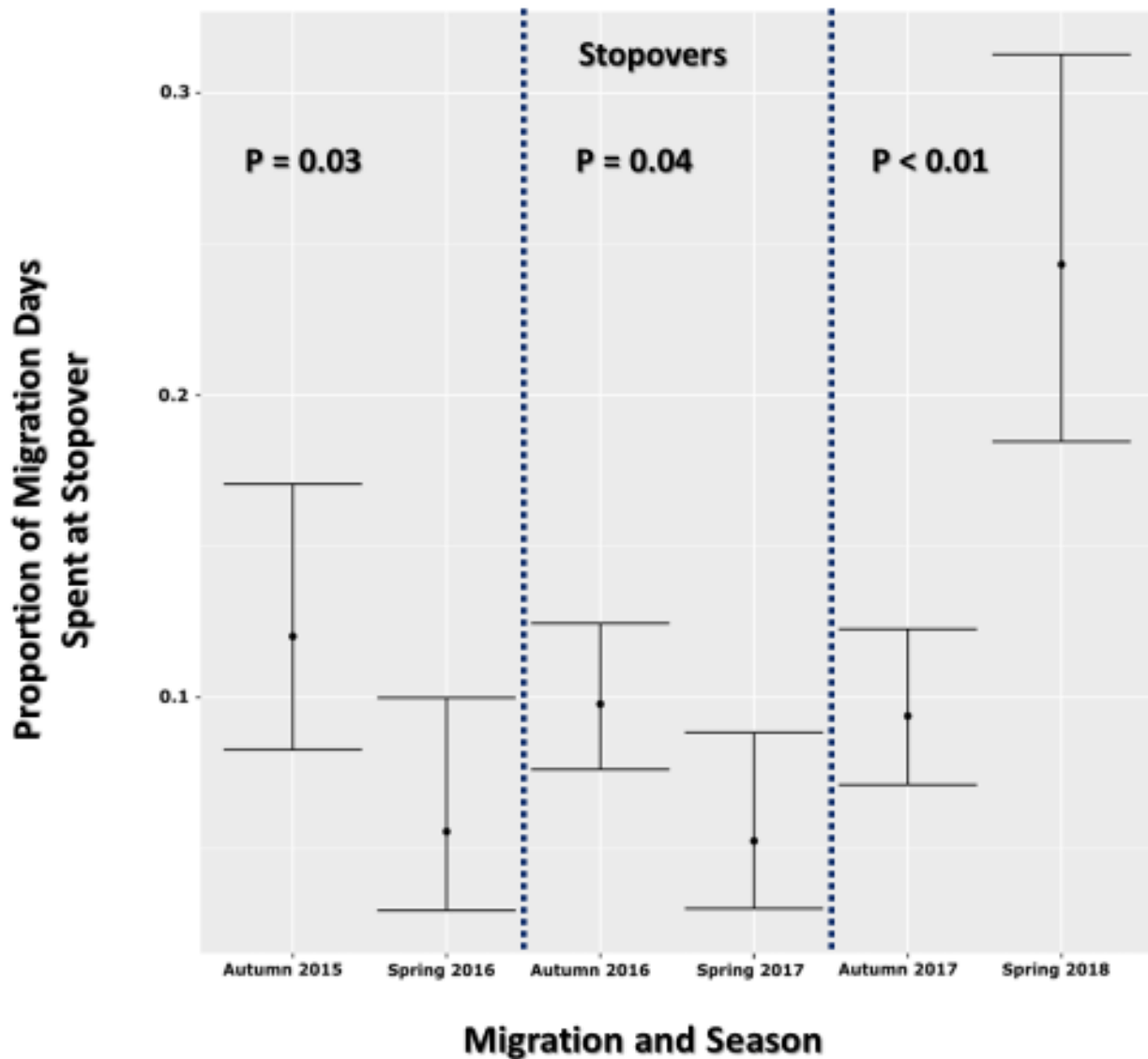


Figure 5. Mean  $\pm$  95% confidence intervals for z-test of the proportion of migration days spent at a stopover for adult female mule deer using a stopover in the Sierra Nevada Mountains, El Dorado County, California, USA (2015-2018). Note: seasons were indicated by time of migrations during a particular autumn to spring seasons that were related by the same winter (for example: Autumn 2015 to Spring 2016). Data was collected from female mule deer over 6 separate migrations; autumn 2015 (n=11), spring 2016 (n=10), autumn 2016 (n=22), spring 2017 (n=21), autumn 2017 (n=23), spring 2018 (n=20).

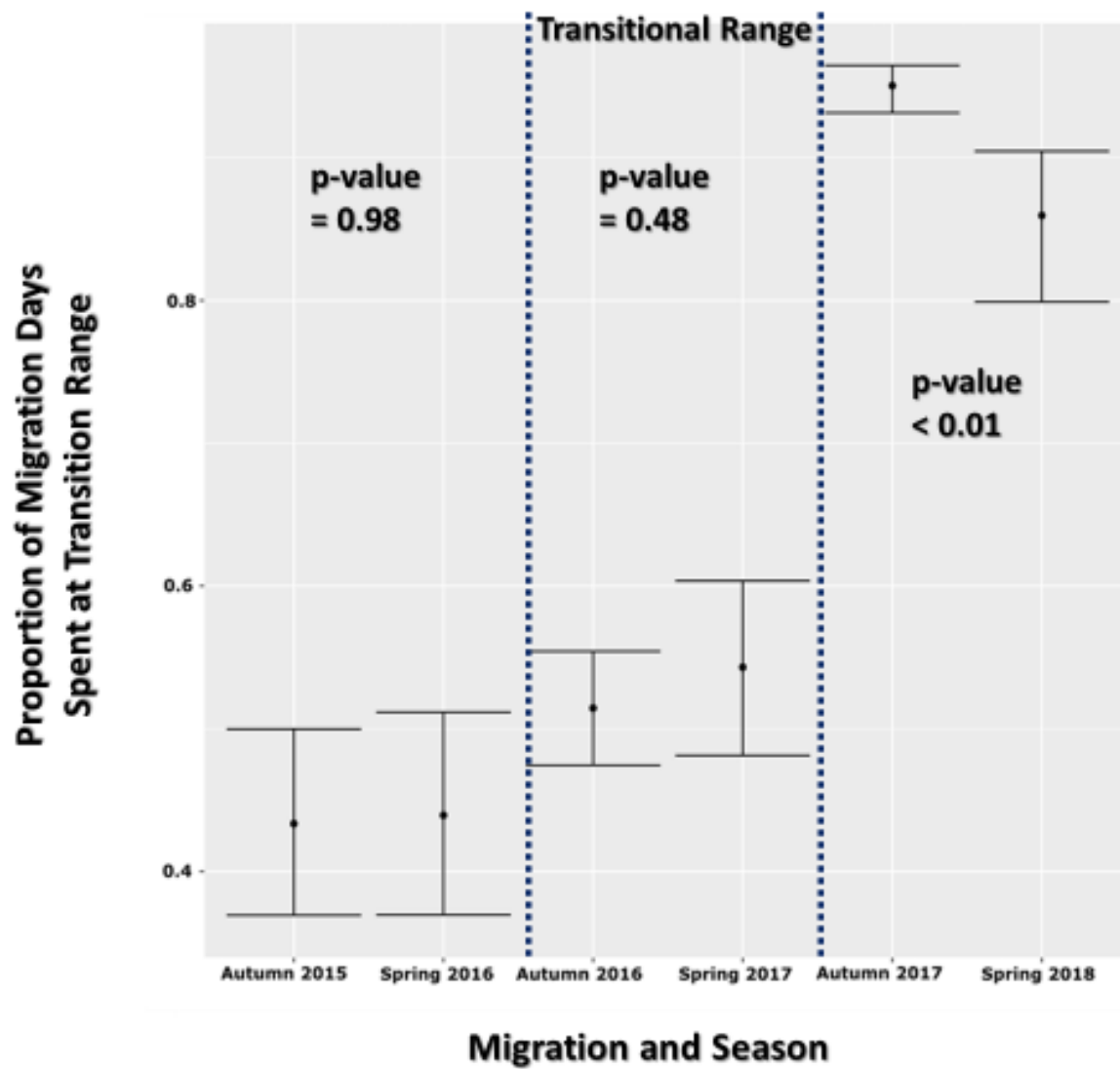


Figure 6. Mean  $\pm$  95% Confidence Intervals for z-test of proportion of use of transitional range during migration by female mule deer in the Sierra Nevada Mountains, El Dorado County, California, USA (2015-2018) Data was collected from female mule deer over 6 separate migrations; autumn 2015 (n=11), spring 2016 (n=10), autumn 2016 (n=22), spring 2017 (n=21), autumn 2017 (n=23), spring 2018 (n=20).

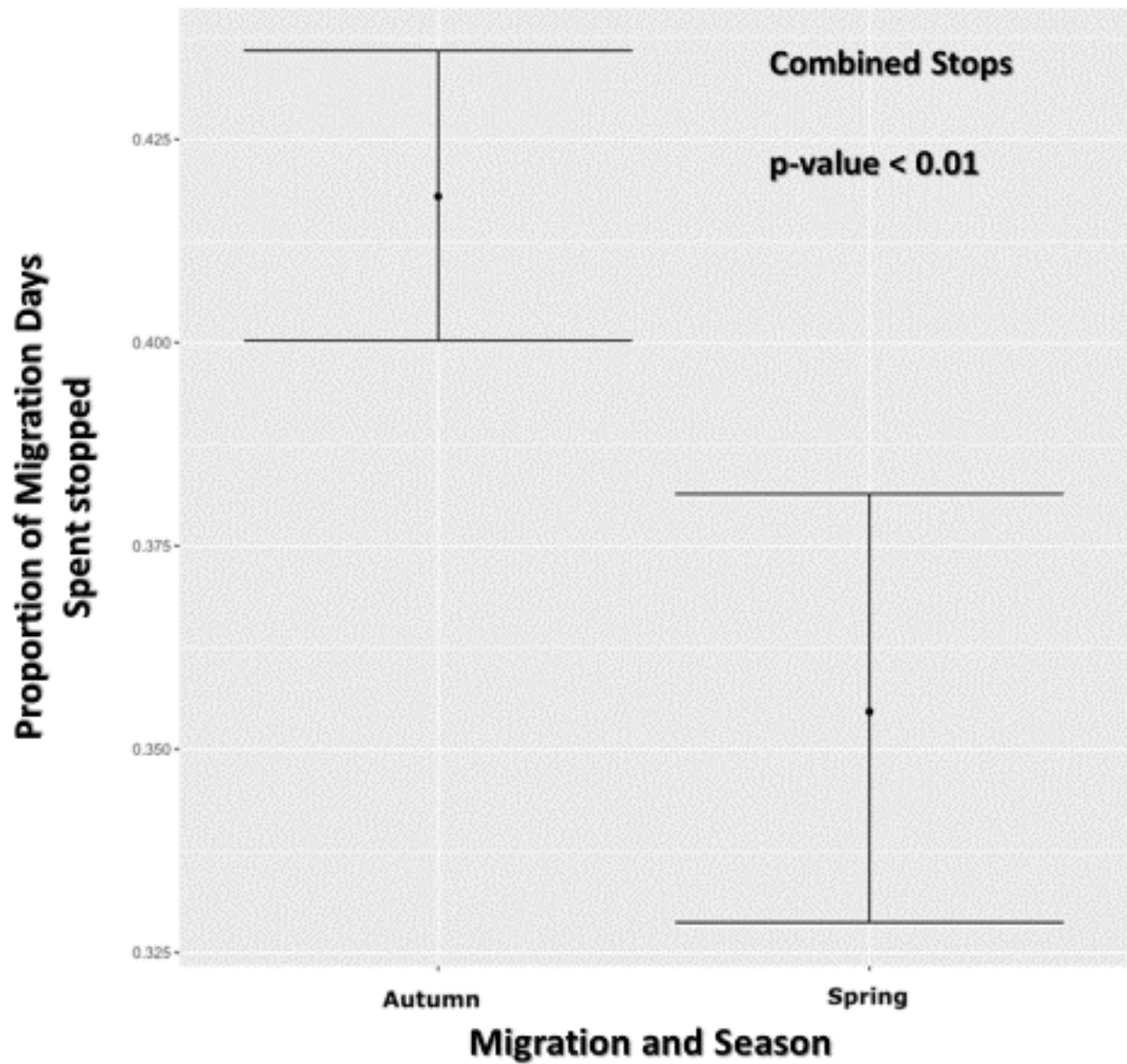


Figure 7. Mean  $\pm$  95% Confidence Intervals for z-test of proportion of days stopped during migration by female mule deer in the Sierra Nevada Mountains, El Dorado County, California, USA (2015-2018) Data was collected from female mule deer over 6 separate migrations; autumn (n=56) spring (n=43).



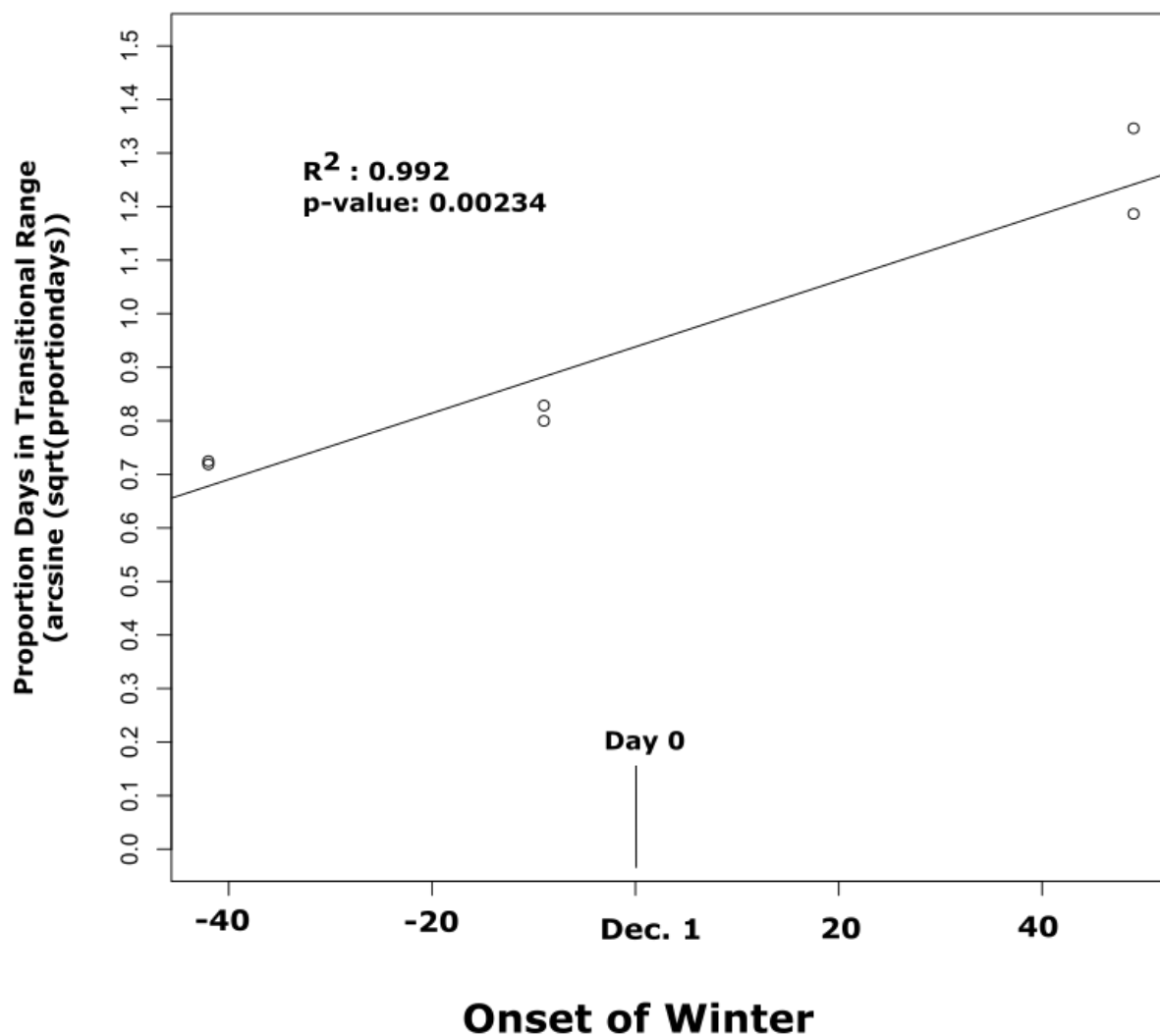


Figure 8. Proportion of days spent in transitional range based on the onset of winter. Proportion of days was transformed using an arcsine square root transformation ( $\arcsine(\sqrt{\text{propdays}})$ ) to fulfill assumptions of normality. Day 0 is December 1<sup>st</sup>. Onset of winter was determined by first day that at least 10mm of snow water equivalent was recorded. If that day was recorded before December 1<sup>st</sup> it was negative and after December 1<sup>st</sup> was positive. Snow water equivalent was recorded by SNOTEL site Robbs Powerhouse El Dorado County, California, USA (elevation 1570 meters).