Sex-specific migratory behaviors in a temperate ungulate

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Abstract. Sexual segregation has been intensely studied across diverse ecosystems and taxa, but studies are often limited to periods when animals occupy distinct seasonal ranges. Some avian and marine studies have revealed that habitat segregation, when sexes differ spatially or temporally in use of the physical landscape, is common during the migratory period and characterized by sex-specific differences in migratory behaviors. Recent research highlights the importance of understanding movement patterns in the context of the full annual life cycle and highlights the need to extend relevant theories of sexual segregation to the migratory period. We tested predictions from two leading hypotheses of sexual segregation, the forage-selection hypothesis (FSH) and the reproductive strategy hypothesis (RSH) as applied to the migratory period. We collected global positioning system (GPS) location data for male and female mule deer (Odocoileus hemionus) in south-central Wyoming and northwest Colorado and tested the main predictions of the FSH and RSH. Both sexes showed high fidelity to their migratory routes, but route fidelity was more variable in males. Males also started spring migrations earlier, ended spring and autumn migrations later, and spent 22% more time on stopover sites during spring migrations. Consequently, males took twice as long in spring and 44% longer in autumn to complete migration. Our results revealed clear sex-specific migratory behaviors and supported predictions of the RSH that male foraging behaviors optimize body condition for the autumn rut, and females prioritize foraging while balancing reproductive constraints. Specifically, males timed their movements with spring green-up as optimally as females, and the timing of male migrations and use of stopovers suggested that males prioritized time in areas of high-quality forage. This refutes predictions of the FSH during the migratory period that males should consistently choose habitats with abundant, low-quality forage. Our findings provide an important contribution to sexual segregation theory by extending relevant theories to understand male and female movements during the migratory period.

Key words: green-wave surfing; habitat segregation; migration; mule deer; Odocoileus hemionus; sexual segregation; ungulate; Wyoming.

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INTRODUCTION

Sexual segregation—when social grouping or space use differs between male and female conspecifics—is common across vertebrate taxa (Ruckstuhl and Neuhaus 2005), especially outside of the breeding season (e.g., birds, Palacin et al. [2009], bats, Senior et al. [2005], reptiles,
Shine et al. [2000], fish, Domeier and Nahsy-Lucas [2012], and ungulates Miquelle et al. [1992]). Habitat segregation, which is one type of sexual segregation, occurs when sexes differ in spatial or temporal use of the physical environment (Conradt et al. 1999). Disparate forage requirements (Clutton-Brock et al. 1982), perceived risk of predation (Main and Coblentz 1996), competition for reproductive sites (Catry et al. 2005), and the physical environment, mainly weather (Conradt et al. 2000), can contribute to habitat segregation (Ruckstuhl and Neuhaus 2005). Most studies to date have isolated empirical tests of habitat segregation to periods when animals occupy seasonal ranges (Ruckstuhl and Neuhaus 2005). However, understanding habitat segregation in the context of the full annual life cycle carries important implications for conservation of migratory species (Marra et al. 2015) and a broadening of sexual segregation theory. Sex-specific behaviors during the migratory period have been addressed in the context of sexual segregation theory for avian (Palacín et al. 2009) and marine species (e.g., Domeier and Nahsy-Lucas 2012). However, despite being one of the most heavily studied groups for sexual segregation (Ruckstuhl 2007), habitat segregation during the migratory period has yet to be evaluated for ungulates in the context of leading hypotheses.

Habitat segregation is pervasive in sexually dimorphic ungulates (Ruckstuhl and Neuhaus 2005) and is observed across seasons (Main 2008), including spring and autumn when most temperate ungulates migrate. Recently, researchers have quantified migratory behaviors in females related to space use, foraging, and time allocation. While some recent studies have evaluated male ungulate migrations (e.g., Debeffe et al. 2019), we still lack a synthetic evaluation of the migration ecology of the sexes. Ungulate migration is largely a strategy to maximize foraging efficiency (Fryxell 1991), or in some instances, minimize predation risk (Fryxell 1995). Advances in GPS technology have facilitated our ability to quantify green-wave surfing (Bischof et al. 2012), the benefits of migration (Middleton et al. 2018), navigation mechanisms (Bracis and Mueller 2017), and migratory tactics (Chapman et al. 2011). Despite these advances, most studies to date have only focused on females due to their importance to population performance (Loison et al. 1999).

After decades of research on the causes of sexual segregation in ungulates, two leading hypotheses have emerged: the reproductive strategy hypothesis (Main and Coblentz 1996) and the forage-selection hypothesis (Ruckstuhl and Neuhaus 2002). The main tenant of the reproductive strategy hypothesis (RSH) posits that males, in preparation for rut and the physical demand of competing for mates, should maximize foraging behaviors that enhance body condition (Main and Coblentz 1996). Females should balance individual resource needs against those needed for offspring survival, using areas of high-quality forage only when within the constraints of securing predator-safe fawning sites (Main and du Toit 2005). The forage-selection hypothesis (FSH) predicts that smaller body size and energetic costs of reproduction (i.e., gestation, lactation, and security sites) drive females to prioritize the use of habitats with higher-quality forage (Barboza and Bowyer 2001). By contrast, larger-bodied males require larger quantities of forage to meet nutritional demands (Illius and Gordon 1987) and therefore should select habitats with increased biomass but lower forage quality (Ruckstuhl and Neuhaus 2002).

Although researchers derived these hypotheses from fundamental principles of foraging and life-history differences between ungulate sexes, neither hypothesis has been tested against sex-specific migratory behavior. Some suggest that the FSH may only be applicable during periods of forage scarcity (Main 2008), but this theory has never been explicitly validated during the migratory period, particularly spring when forage is abundant. With the recent development of green-wave surfing as a metric that quantifies optimal foraging during migration (Bischof et al. 2012), we can now compare detailed foraging behaviors between sexes of migratory ungulates. The green-wave hypothesis predicts that during spring migrations, herbivores will time their movements with, or surf, vegetation of intermediate biomass as it gradually becomes available along increasing elevations or latitudes (Drent et al. 1978, Bischof et al. 2012). In order to capitalize on the availability of this ephemeral resource, female mule deer synchronize their movements with the emergence of spring green-up and
spend a disproportionate amount of time in stopover sites where green-up is at its peak (Sawyer and Kauffman 2011). Whether males exhibit the same behavior has yet to be tested. Here, we tested the RSH and FSH in the context of ungulate migration for the first time. Under the RSH, we would expect males during migration to meet high nutritional demands by surfacing waves of spring green-up as well as or better than females, who may be focused on the impending need to secure safe sites for offspring (Main and du Toit 2005). Conversely, under the FSH, males should migrate later, behind the wave of green-up when forage biomass is more abundant, but more fibrous and less palatable (Fryxell 1991).

Other well-studied migratory behaviors can also help us understand whether sexes segregate in migratory or foraging behaviors. Firstly, migratory fidelity is an indicator of whether following established migration routes, switching to resident behavior, or modifying migration routes provides an adequate response to environmental conditions (Chapman et al. 2011, Sawyer et al. 2019). Secondly, migration distance can be interpreted as individual access to unique and potentially unexploited summer range sites (Charnov 1976). Additionally, the timing and duration of migration are metrics of individual response to weather (Pettorelli et al. 2005), plant phenology and abundance (Hebblewhite et al. 2008), and time spent foraging along the migration route (Bischof et al. 2012). Lastly, time spent in stopover sites indicates individual time allocated to foraging along the migratory route vs. directed movement toward summer range (Sawyer and Kauffman 2011).

We studied a migratory herd of mule deer (a species with pronounced sexual body size dimorphism; Wallmo 1981) in south-central Wyoming and northwest Colorado where deer migrate seasonally between low-elevation winter range and high-elevation summer ranges. We characterized sex-specific migratory behaviors using bi-hourly GPS-location data. For individuals of both sexes, we measured route fidelity, migration distance, timing and duration of migration, stopover use, and green-wave surfing. For each metric, we tested for differences between males and females across years and seasons and interpreted results in the context of predictions arising from the application of the RSH and FSH hypotheses to the phenomenon of migration.

**Materials and Methods**

**Study area**

Our study area in south-central Wyoming and northwest Colorado (41°19.1’ N, -107°41.6’ W) was a heterogeneous landscape of lowland sagebrush (Artemesia sp.) steppe, mixed-shrub foothills, montane forest, and high-alpine tundra. Winter habitat was dominated by sagebrush, mixed shrubs (Sarcobatus vermiculatus, Purshia tridentata, Amelanchier sp.), and pinyon-juniper (Juniperus sp.). Foothills were mostly gamble oak (Quercus gambelii) and aspen (Populus tremuloides), and mountains were dominated by lodgepole pine (Pinus contorta), aspen, and Engelmann spruce (Picea engelmannii). We studied a mule deer population that migrates 20–170 km from a common lower elevation winter range (1900–2200) to various higher elevation (2400–3435 m; Fig. 1) summer ranges (Sawyer et al. 2009, 2013).

The Bureau of Land Management (BLM) managed most winter range, and all deer crossed lands of multiple ownership during migration, including private, BLM, State of Wyoming, and U.S. Forest Service. From 2016 to 2018, the Baggs deer herd of around 20,000 ± 1500 (± SD) individuals, provided nearly 15,000 ± 1700 hunter days and yielded around 1700 ± 500 deer harvests annually (Mong 2016, Stephens 2017, Damm 2018).

**Animal capture and movement data**

We used helicopter net-gunning to capture 95 adult (≥ 2.5 yr of age) male and 32 adult female (≥ 1.5 yr of age, n = 32) deer over three separate winters between December 2015 and February 2017. All animals were handled in accordance with the Institutional Animal Care and Use, Model Wildlife Protocol (Number 20190301MK00347-01). We affixed an Iridium (Iridium Communications McLean, Virginia, USA) or Globalstar (Globalstar, Covington, Louisiana, USA) satellite-enabled GPS collar (Advanced Telemetry Systems, Isanti, Minnesota, USA; Lotek Wireless, Newmarket, Ontario, Canada) to males, which allowed for neck expansion during the autumn rut. We outfitted females with a GPS- or Globalstar satellite-enabled GPS collar (Telonics, Mesa, Arizona, USA). We
programmed 30 collars on males to collect one location/hour, and another 65 collars for males and 32 collars for females were programmed to collect one location every two hours. Fix rates were consistent regardless of animal movement (e.g., migratory vs. stopover).

**Metrics of migratory behavior**

We defined a common winter range (~17,000 ha; Fig. 1) where both males and females spent winter months (December–March) or stopped over for more than 24 h before continuing their winter movements (up to 65 km) in years with heavy snowfall. We evaluated five metrics of migratory behavior for sex-specific differences, including (1) route fidelity, (2) migration distance, (3) migration timing, (4) time spent at stopover sites, and (5) green-wave surfing. We identified autumn and spring migration sequences using net-squared displacement (Bunnefeld et al. 2011) and verified by visual inspection of mapped GPS locations and dates. We standardized fix rates for each individual to one fix every four hours. Given that timing of migration may vary widely across years for individual animals (e.g., Monteith et al. 2011), we treated individual migrations as unique samples in our analysis of timing and duration, stopover use, and green-wave surfing.

Fig. 1. Male and female mule deer migration routes in south-central Wyoming and northwest Colorado, USA, 2016–2018.
Fidelity.—Following the approach of Sawyer et al. (2019), we estimated 99% utilization distributions (UD) for individual spring and autumn migratory routes for the first year of migration ($t$), using the Brownian bridge movement model (BBMM; Horne et al. 2007). We measured fidelity of each successive migration ($t+1$), by calculating the percentage of GPS locations that fell within the 99% contour of the UD at year $t$ (Sawyer et al. 2019). We estimated fidelity of spring migrations to the first spring migration for each individual and, separately, fidelity of autumn migrations to the first autumn migration (Sawyer et al. 2019). We then fit a mixed-effects linear model from R package lme4 (R Version 4.0.2), with fidelity as the response variable and sex as the predictor variable or fixed effect, and we assigned individual animals as random intercepts and slopes. Lastly, we used a one-way analysis of variance (ANOVA) to evaluate differences between our fitted model and a reduced model without sex as a fixed effect.

Distance.—To evaluate whether sexes differed in distance travelled, we first calculated the Euclidian distance (km) along the sequence of locations between winter and summer ranges for each individual. We measured distance between locations and small clusters (~10 or fewer points) of locations in the direction of the appropriate seasonal range (e.g., movements toward summer range in spring). At point clusters of ~10 or more points, mainly stopover sites, we measured the diameter of the cluster and added this to the total distance. Individual migration distances are generally consistent across years in female mule deer (Sawyer and Kauffman 2011). However, to account for any potential variation in migration distance within individuals, we used a mixed-effects linear model from R package lme4 (R Version 4.0.2) with distance as the response variable and sex as a predictor or fixed effect, and we assigned individual animals as a random intercepts and slopes. Lastly, we used a one-way analysis of variance (ANOVA) to evaluate differences between our fitted model and a reduced model without sex as a fixed effect.

Timing and duration.—To test for differences in migration timing, we first identified the start and end of spring and autumn migration by extracting the ordinal day of the first and last locations of spring and autumn migration sequences. We then calculated duration as the number of days between the start and end of migration. Lastly, we tested for differences in migration timing between sexes and across years and seasons using a parametric $t$-test.

Stopover use.—We defined stopover sites as the upper 10% quantile of the utilization distribution from the BBMM (Sawyer et al. 2009), using dynamic BBMM (Kranstauber et al. 2012) for ease and speed of processing. We then generated raster contours of stopovers for each migratory event (e.g., deer 29, spring, 2016) and estimated the time spent in stopovers as the percent of GPS locations from the respective migratory period that fell within the contour. Lastly, we tested for differences in stopover use between sexes across seasons for data from all years using a parametric $t$-test.

Green-wave surfing.—We followed methods outlined by Aikens et al. (2017) to quantify surfing between the sexes and to test for differences in surfing ability (Appendix S1). For each deer and year, we quantified the two most informative metrics of surfing using the instantaneous rate of green-up (IRG), or the first derivative of a double-logistic curve of time-series data for the Normalized Difference Vegetation Index (NDVI; MOD09Q1; 250-m spatial resolution, 8-d temporal resolution); (1) the average IRG each individual experienced during spring migration and (2) the mean number of days from peak IRG (days from peak or DFP; Aikens et al. 2017). These metrics provide a complimentary view of surfing, with IRG experienced reflecting phenological dynamics and deer movement, while DFP reflects deer behavior relative to the wave of spring green-up (Aikens et al. 2017, Middleton et al. 2018). For IRG, we used linear regression to estimate the slope from the date of peak IRG and the date each deer used that same location during the spring green-up period (i.e., date occupied). We tested for differences between sexes in DFP using a parametric $t$-test and 95% confidence (2SE).

Surfing by mule deer is strongly influenced by the pace and pattern of plant phenology, or the greenscape that each animal migrates along (Aikens et al. 2017). To account for differences in the phenological landscape, we quantified three metrics that characterize the greenscape following the methods of Aikens et al. (2017): the order,
rate, and duration of green-up (Appendix S1). Our primary method for comparing surfing between sexes while accounting for the effects of the greenscape was to model DFP as a function of each greenscape metric and sex across all years using linear regression. We also compared whether males or females occupied routes with distinct greenscape characteristics (i.e., the phenological quality of the route) using a parametric $t$-test and 95% confidence (2SE) for each greenscape metric between sexes.

RESULTS

Migratory behaviors varied across year and season for male and female mule deer. Seven males were resident and did not migrate—we excluded these individuals as well as data from fifteen collars that malfunctioned during the first migratory period (Spring 2016). Sample sizes varied given the requirements of the model or statistical tests used in each analysis (see Appendix S2: Table S1 for a complete list of sample sizes used to analyze each metric for each sex).

**Fidelity**

We found no evidence for sex-specific differences in mean fidelity to migratory routes in spring ($\beta$ for male fidelity = −0.12, SE = 0.06, 95% CI = −0.248–0.001) or autumn ($\beta$ for male fidelity = −0.06, SE = 0.09, 95% CI = −0.25–0.14), although males exhibited wider variation in individual fidelity across both seasons (Fig. 2). Additionally, our primary model including individual as a random effect and sex as a fixed effect vs. the reduced model without sex as a variable explained 95% of the variation in migration distance ($\sigma^2_{\text{res}} = 444, N_{\text{ID}} = 83$). Additionally, our primary model including individual as a random effect and sex as a fixed effect (AIC = 1592.1) and the reduced model without sex as a variable (AIC = 1591.4) were similar ($\Delta$AIC < 2).

**Timing and duration**

The start and end of migratory periods varied across years and seasons (Fig. 3c). The average start date of male migrations in spring ($n = 67$) was $107 \pm 2$ d ($\bar{x} \pm 95\%$ CI) and $111 \pm 3$ d for female migrations in spring ($n = 55$). Across years, males started spring migrations earlier than females ($\alpha = 0.05$, $t = -2.45$, df = 95, $P = 0.02$). The average end date of male migrations in spring was $131 \pm 4$ d ($\bar{x} \pm 95\%$ CI) and $124 \pm 4$ d for females. Across years, males ended spring migrations later than females ($\alpha = 0.05$, $t = 2.85$, df = 120, $P = 0.005$). Overall, males spent twice as much time migrating in spring ($\bar{x} = 24 \pm 3$ d) compared with females ($\bar{x} = 12 \pm 4$ d; $\alpha = 0.05$, $t = 4.93$, df = 115, $P < 0.001$). In autumn, the average start date of male migrations ($n = 34$) was $294 \pm 8$ d ($\bar{x} \pm 95\%$ CI) and $297 \pm 10$ d for female migrations ($n = 49$). The average end date for male migrations in autumn was $350 \pm 12$ d ($\bar{x} \pm 95\%$ CI) and $336 \pm 5$ d for female migrations. Across years, start dates of male and female migrations in autumn were similar ($\alpha = 0.05$, $t = -0.54$, df = 81, $P = 0.59$), but male migrations ended later ($\alpha = 0.05$, $t = 2.15$, df = 46, $P = 0.04$). Overall, males spent 44% more time migrating in

![Fig. 2. Average fidelity (percent) and 95% confidence intervals of mule deer to their first migratory routes in spring (b) and autumn (c). We studied a herd of mule deer in south-central Wyoming and northwest Colorado, USA, 2016–2018.](image)
autumn (56 ± 10 d) compared with females (X = 39 ± 14 d, t = 2.08, df = 65, P = 0.04).

**Stopover use**

Stopover use and the duration of migration were correlated (Pearson correlation, r = 0.68, t = 10.2, df = 120, P < 0.001). However, we included both metrics given their relevance for understanding differences between sexes in migration distance and timing. Overall, in spring, male mule deer spent 77 ± 7% (X ± 95% CI) of the migration period in stopovers, while females spent 55 ± 8% of migration time in stopovers (Fig. 3b). Overall, male migrations in spring (n = 29) were characterized by more time in stopovers than female migrations in spring.
(n = 37; t = 3.97, df = 64, P < 0.001). Overall, in autumn, males spent 78 ± 11% of migration time in stopovers compared with 72 ± 10% in females. Time in stopover sites during autumn was similar between male (n = 23) and female (n = 33) migrations (t = 0.82, df = 49, P = 0.42).

**Green-wave surfing**

Nearly all deer from our study surfed, as measured by average days from peak green-up (DFP; Fig. 4d) and ability to track peak IRG (Fig. 4e–g). Although the FSH predicted males to migrate behind the green wave to acquire higher forage abundance, they surfed as well as females across metrics (Fig. 4). Average DFP was similar for males (23 ± 2 DFP) and females (24 ± 2 DFP), parametric t-test, t = −0.191, df = 81, P = 0.85, n = 87 total migration sequences, n = 61 total individuals) across years (Fig. 4, d). The surfing of both sexes was significantly influenced by green-up order (β = −8.39, SE = 1.72, t = −4.89, P < 0.001) and duration (β = −3.75, SE = 0.67, t = −5.90, P < 0.001) but not rate (β = −3.45, SE = 2.85, t = −1.21, P = 0.23; Fig. 4a–c). None of the greenscape metrics differed between male and female routes (Fig. 4h).

**DISCUSSION**

We found broad evidence for sex-specific differences and habitat segregation during the migratory period of mule deer, contributing to decades of testing sexual segregation theory (Ruckstuhl and Neuhaus 2005, Main 2008). We found support for the reproductive strategy hypothesis (RSH), mainly that males and females move similarly to optimize foraging in spring habitats when high-quality forage is available. Males and females showed high fidelity to established migration routes and migrated similar distances on average, but male fidelity and migration distance were more variable. Additionally, male and female mule deer differed in the pace and timing of their spring and autumn migrations. Specifically, males started and ended migrations at different times in spring, ended migrations later in autumn, took longer to complete their migrations overall, and spent more time at stopover sites in spring. Females tracked the progression of spring green-up, as has been previously shown (Merkle et al. 2016).

Interestingly, males surfed the green wave as well as females. Our finding that males move to optimize their access to high-quality forage is consistent with the predictions of the RSH; we did not find support for predictions of the forage-selection hypothesis (FSH) during periods of forage abundance.

Although both sexes tended to use the same migratory routes year after year, we found route fidelity was more variable with males. Higher variability in route fidelity suggests males may be more plastic in their migratory tactics compared with the more rigid movements of females (e.g., Sawyer et al. 2019). Young mule deer may exhibit exploratory behaviors after their first year (Mackie et al. 2003). For example, Jakopak et al. (2019) documented a female yearling that moved 94 km in 15 d away from the summer range of her mother. Such movements strongly suggest migratory learning is more complex than young animals simply learn routes from their mothers (e.g., Jesmer et al. 2018). Relatedly, variability in migratory fidelity observed in our study suggests there may be opportunities for non-maternal or independent learning in the adult male segment of the population as well. It is possible, for example, that males learn alternate routes from other males in bachelor groups (Mackie 1970), similar to how adult bison (Bison bison) teach each other where to find the best forage in the local environment (Merkle et al. 2015). Furthermore, the seven males from our study that were residents suggest that males could have garnered some sort of fitness advantage from resident behavior (e.g., blackbirds, Zúñiga et al. 2017). We find this unlikely given that partial migration and residency are common among populations of female ungulates (Chapman et al. 2011). Understanding the mechanisms behind migratory plasticity is emerging as an important research topic (Berg et al. 2019) with strong conservation implications (Sawyer et al. 2019).

Although the range of migration distances was wider in males (10–151 km) than females (8–78 km), average migration distance was similar between sexes. Migration distances of females were typical of other females in the region (Sawyer and Kauffman 2011, Lendrum et al. 2014). Given that females in other study areas migrate longer distances of up to 240 km, the males we observed migrating farther distances may have
Fig. 4. Green-wave surfing as measured by days from peak (DFP) instantaneous rate of green-up (IRG) and
been a product of our sampling distribution. However, the pattern of males migrating farther should not be discounted, given several recent studies have found longer-distance migrations in male ungulates (e.g., moose \(Alces alces\), Bunnefeld et al. 2011) and that differential migration distance is a common phenomenon in other taxa (e.g., birds, sharks, Ruckstuhl and Neuhaus 2005).

Males initiated spring migrations earlier, spent more time at stopover sites, and arrived at summer and winter range later; thus, males spent more time migrating overall. Numerous studies have found differences between sexes in timing of migrations in ungulates (mule deer, Kucera [1992]; red deer, Debeffe et al. [2019]; moose, Bunnefeld et al. [2011]; elk, McCorquodale [2003]; and roe deer, Cagnacci et al. [2011]) and other taxa (e.g., birds, Catry et al. [2005]). We did not observe timing consistent with predictions under the FSH (Table 1). Consistent with the RSH, more time for males at stopover sites in spring suggests that males are foraging more along the route (Sawyer and Kauffman 2011). Arriving at summer range earlier may be a strategy for females trying to avoid giving birth along the migratory route, which could restrict movements (e.g., Bischof et al. 2012). Snow and weather events can sometimes trigger autumn and spring migrations (Monteith et al. 2011). By arriving at winter range earlier in autumn or leaving later in spring, females and their accompanying offspring can avoid the energetic costs of moving through deep snow (Parker et al. 1984). The taller chest heights of males, however, enable them to move through deeper snow (Telfer and Kelsall 1984) and thus increase time spent foraging at higher elevations before descending to winter range. By doing so, males might benefit from exploiting resources of superior forage quality for longer and avoid competition with conspecifics (Murray and Illius 2000).

In autumn, our findings that migration start dates and time in stopovers were similar between sexes suggest that the factors that led our observed differences in spring (e.g., forage quality) may be less active in autumn or entirely different (e.g., autumn rut).

Both sexes in our study surfed the green wave, although some males surfed better, likely because of their increased energy requirements. Depletion of energy reserves from strenuous rutting activities and reduced foraging time (Bowyer 1981) coupled with over-winter fat loss (Parker et al. 2009) in male ungulates leaves them in poor condition when spring arrives (Klein 1965). By optimally surfing, males can compensate for the energetic costs of rut and winter (Koga and Ono 1994), replenish lost fat, and support antler growth (Robinette et al. 1973, Barboza and Bowyer 2001). Concomitantly, surfing could preemptively build muscle tissue and fat reserves for the autumn rut (Main et al. 1996), which directly correlates with reproductive success, odds of individual survival, and lifetime fitness (Clutton-Brock et al. 1980, Main and Coblentz 1996). Surfing is inherently challenging because it requires that ungulates time their movements precisely with plant phenology (Bischof et al. 2012). Despite its challenges, our results and those from Aikens et al. (2017) show that female mule deer are fully capable of surfing waves of spring green-up during migration. However, because females balance a trade-off between finding high-quality forage and increasing security from predators or human disturbance (consistent with the RSH; e.g., Bleich et al. 1997, Main 2008), there are likely instances where...
reproduction constrains the ability of females to surf as optimally as males.

Overall, these findings refute predictions of the forage-selection hypothesis (FSH) when applied to the migratory period that males should consistently prefer habitats with relatively high biomass, low-quality forage (Main et al. 1996). This bolsters support for the idea that the FSH is only applicable during periods of forage scarcity (i.e., winter, drought) when male ungulates may sacrifice quality for quantity (Ruckstuhl and Neuhaus 2002), because they are more efficient at digesting low-quality forage than females (van Soest 1994). Moreover, the literature is clear that there is no known selective force that would lead males to avoid abundant, high-quality resources that directly improve body condition and reproductive success (Main 2008). This helps to explain why predictions of the reproductive strategy hypothesis (RSH) held during the migratory period, primarily because males used areas that maximized their foraging opportunities (Main and Coblentz 1996).

Recent work predicts that habitat suitability and the response of ungulates to warming climates will vary by species (Parmesan 2006) and sex (Rivrud et al. 2019). In the face of increased climate variability and habitat loss (Powers and Jetz 2019), the larger migratory ranges of male mule deer, their ability to optimize foraging, and their resilience to weather variables like deep snow may lead to migratory persistence. Alternatively, the unique migrations required by males may increase their vulnerability to landscape changes. For example, migratory corridors of individuals who travel farther distances are likely to be more constrained by human

| Metric               | Relevant hypotheses                                                                 | Predictions                                                                 | Justification or supporting literature                                                                 |
|----------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------|
| Fidelity             | No direct relationship to hypotheses                                                 | High fidelity in M and F                                                  | F showed high fidelity in Sawyer et al. (2019)                                                       |
| Distance             | No direct relationship to hypotheses                                                 | M ~ F or M > F                                                           | M > F in some ungulates (e.g., moose, Bunnefeld et al. 2011)                                         |
| Timing and duration  | Reproductive Strategy Hypothesis (RSH)                                              | (Spring) M and F leave around same time; F arrive earlier                 | (Spring) M and F match timing with best forage; F may be restricted by fawning                       |
|                      | Forage-selection Hypothesis (FSH)                                                    | (Autumn) M leave later and arrive later than F                            | (Autumn) M maximize time in high-quality forage sites above winter range; F may be restricted by fawns and weather |
|                      |                                                                                      | (Spring) M leave later and arrive later than F                            | (Spring) M delay departure from winter range where forage biomass is higher, then leave later when peak forage biomass occurs along migration route |
|                      |                                                                                      | (Autumn) Unclear                                                         | (Autumn) M use sites with highest forage biomass and F use sites with higher-quality forage, both presumably on summer range or migration route (Sawyer and Kaufman 2011) |
|                      | Time in stopovers                                                                     | (Spring) M > F or M ~ F                                                  | (Spring) M and F prioritize foraging; F may be restricted by fawns                                   |
|                      | Forage-selection Hypothesis (FSH)                                                    | (Autumn) M > F or M ~ F                                                  | (Autumn) M and F prioritize foraging; F may be restricted by fawns                                   |
|                      |                                                                                      | (Spring) Unclear                                                         | M prioritize forage quantity. F prioritize quality. Both could meet these requirements by spending more time on stopovers |
|                      | (Autumn) Unclear                                                                      | M prioritizes forage quantity. F prioritizes quality. Both could meet these requirements by spending more time on stopovers |
|                      | Green-wave surfing                                                                    | M ~ F or M > F                                                           | M and F prioritize foraging in high-quality habitats; F may be restricted by fawns.                  |
|                      | Forage-selection Hypothesis (FSH)                                                    | M < F                                                                    | F selects habitats with high-quality forage; M selects habitats with high forage quantity but low quality |

Note: Supported predictions or hypotheses are in bold, unsupported are in italics, and unknown are in regular type font.
developments and associated infrastructure (Berger 2004). Disturbances from developments can amplify stress and speed up movement rate (Sawyer et al. 2013, Wyckoff et al. 2018), thus inhibiting surfing ability or other foraging behaviors. While we typically do not consider ungulate populations to be male-limited (Mysterud et al. 2002), decreased landscape connectivity can be deleterious for gene flow (Boulet et al. 2007). The notion that females balance trade-offs associated with foraging and reproduction is well established (Main 2008). Compounding these intrinsic factors with those of climate change and increasing human disturbance (e.g., Sawyer et al. 2017) will require increased attention to the mobility of populations to be male-limited (Mysterud et al. 2002), decreased landscape connectivity can be deleterious for gene flow (Boulet et al. 2007). The notion that females balance trade-offs associated with foraging and reproduction is well established (Main 2008). Compounding these intrinsic factors with those of climate change and increasing human disturbance (e.g., Sawyer et al. 2017) will require increased attention to the mobility of populations of female ungulates. As human-dominated ecosystems become increasingly complex, efforts to improve connectivity of landscapes based on sex-specific requirements will be necessary for managing populations of migratory ungulates.

This work brings us closer to a more general theory of sexual segregation in ungulates that is applicable to migration. First, by supporting the RSH, our results reveal that behaviors important to reproduction and survival are active during non-migratory and migratory seasons (Main 2008), providing a more complete picture of habitat segregation during the full annual life cycle (Marra et al. 2015). Our work agrees with broader sexual segregation theory across taxa that existing hypotheses for sexual segregation theory apply to some species but not others and that reasons for sexual segregation are species-specific (Ruckstuhl and Neuhaus 2005). Additionally, our finding that males surf as well or better than females suggests that sexual segregation hypotheses pointing to body size differences as ultimate explanations for habitat segregation (i.e., FSH; Ruckstuhl and Neuhaus 2002) are unfounded. The prominent environmental factors and behaviors that influence segregation in spring (e.g., forage quality and anti-predatory movements) as well as aggregation in autumn (e.g., precipitation events and mate-finding) are pronounced during the migratory period (Main and du Toit 2005, Avgar et al. 2014). For this reason, and because we now know that migratory behaviors are sex-specific in mule deer, the migratory period is ideal for testing the mechanisms of habitat segregation. Importantly, this provides a conceptual framework for new research focused on sexual segregation during migration.

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