

# Stopover ecology of a migratory ungulate

Hall Sawyer<sup>1,2\*</sup> and Matthew J. Kauffman<sup>3</sup>

<sup>1</sup>Department of Zoology and Physiology, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071, USA; <sup>2</sup>Western Ecosystems Technology, Inc., 200 South 2nd St., Laramie, WY 82070, USA; and

<sup>3</sup>Department of Zoology and Physiology, United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY, USA

## Summary

1. Birds that migrate long distances use stopover sites to optimize fuel loads and complete migration as quickly as possible. Stopover use has been predicted to facilitate a time-minimization strategy in land migrants as well, but empirical tests have been lacking, and alternative migration strategies have not been considered.

2. We used fine-scale movement data to evaluate the ecological role of stopovers in migratory mule deer *Odocoileus hemionus* – a land migrant whose fitness is strongly influenced by energy intake rather than migration speed.

3. Although deer could easily complete migrations (range 18–144 km) in several days, they took an average of 3 weeks and spent 95% of that time in a series of stopover sites that had higher forage quality than movement corridors. Forage quality of stopovers increased with elevation and distance from winter range. Mule deer use of stopovers corresponded with a narrow phenological range, such that deer occupied stopovers 44 days prior to peak green-up, when forage quality was presumed to be highest. Mule deer used one stopover for every 5.3 and 6.7 km travelled during spring and autumn migrations, respectively, and used the same stopovers in consecutive years.

4. Study findings indicate that stopovers play a key role in the migration strategy of mule deer by allowing individuals to migrate in concert with plant phenology and maximize energy intake rather than speed. Our results suggest that stopover use may be more common among non-avian taxa than previously thought and, although the underlying migration strategies of temperate ungulates and birds are quite different, stopover use is important to both.

5. Exploring the role of stopovers in land migrants broadens the scope of stopover ecology and recognizes that the applied and theoretical benefits of stopover ecology need not be limited to avian taxa.

**Key-words:** Brownian bridge movement model, migration routes, movement corridors, mule deer, *Odocoileus hemionus*, phenology, stopover ecology, ungulate migration

## Introduction

With the exception of orientation and navigation capacity, the ability of animals to complete long-distance migrations is largely determined by the energetic requirements needed to fuel migratory movements (Alerstam, Hedenström & Åkesson 2003). Animals use a wide variety of adaptations to meet these energetic requirements, including changes in morphology, physiology and behaviour (Ramenofsky & Wingfield 2007). Across taxa, some species display all three of these traits (e.g. birds), while others may exhibit only behavioural changes (e.g. ungulates). A common behavioural strategy

among all long-distance migrants is their use of stopover sites – habitat patches along the migration route where animals rest and forage to renew energy reserves (Dingle & Drake 2007). The study of stopover sites, or ‘stopover ecology’, has become an area of intense research in avian ecology (Newton 2008), with particular emphasis on optimal migration strategies (Erni, Liechti & Bruderer 2002), energetics (Weber & Houston 1997) and predation risk (Pomeroy, Butler & Ydenberg 2006). To date, stopover ecology has been largely ignored in migratory taxa whose mode of locomotion is running or swimming (but see Hedenström 2003a).

The ecological role of stopovers in avian taxa is directly related to their migration strategy, which for most long-distance migrants, is one of time-minimization (or speed-

\*Correspondence author. E-mail: hsawyer@west-inc.com

maximization) whereby birds attempt to migrate from wintering areas to breeding grounds in the shortest time possible (Alerstam & Hedenström 1998; Hedenström 2008). The fitness benefits of this migration strategy are linked to the ability of early-arriving birds to find mates, establish high-quality territories and nest successfully (Weber & Houston 1997). Stopover sites are considered a key component in this type of migration because the rate of fuel accumulation determines the overall migration speed (Åkesson & Hedenström 2007). Because carrying heavy fuel reserves increases transport cost regardless of locomotion mode, time-minimization has been proposed as a likely migration strategy across migratory taxa (Åkesson & Hedenström 2007), including those that run or walk (Alexander 1998; Alerstam, Hedenström & Åkesson 2003; Hedenström 2003b). This prediction assumes that optimizing fuel loads and minimizing transport cost is a primary constraint of migration for animals, regardless of their mode of locomotion.

Ungulates are perhaps the most notable land migrants, and recent work has identified stopover use along migratory paths (Sawyer *et al.* 2009), patterns that are consistent with previous modelling efforts aimed at identifying behavioural states of ungulate movements (Johnson *et al.* 2002; Franke, Caelli & Hudson 2004; Morales *et al.* 2004). But the presumed benefits of time-minimization migration have not been reconciled with the well-documented foraging strategy of ungulates, which is to maximize energy intake during the growing season (McNaughton 1985; Wilmschurst *et al.* 1999; Fryxell, Wilmschurst & Sinclair 2004; Holdo, Holt & Fryxell 2009). Specifically, completing seasonal migrations in the shortest amount of time offers no obvious fitness benefits to ungulates. In contrast to birds, the migratory locomotion of ungulates is unlikely to be constrained by heavy fuel loads (Parker, Robbins & Hanley 1984), and fitness is instead strongly influenced by fat accumulation during the growing season (Hobbs 1989; Cook *et al.* 2004; Bishop *et al.* 2009; Parker, Barboza & Gillingham 2009). Thus, stopover use to maximize migration speed is only likely for ungulates if it allows individuals to maximize the intake of high-quality forage during the growing season. For ungulates, maximum energy intake occurs when forage plants are less mature and highly digestible, but developed enough that intake is not constrained by cropping time (Hebblewhite, Merrill & McDermid 2008). Tropical ungulates achieve this by aggregating in large herds that keep forage at an immature but highly nutritious growth stage (Fryxell 1991) and by migrating in response to phenology gradients created by rain-autumn patterns (e.g. wildebeest *Connochaetes taurinus*; Boone, Thirgood & Hopcraft 2006; Holdo, Holt & Fryxell 2009). In contrast, temperate ungulates such as elk *Cervus elaphus* migrate along phenology gradients created by elevation and topography (Hebblewhite, Merrill & McDermid 2008). Existing evidence suggests that a general strategy of migratory ungulates is to follow the most nutritious vegetation to maximize energy intake during the growing season (McNaughton 1985; Wilmschurst *et al.* 1999; Fryxell,

Wilmschurst & Sinclair 2004; Holdo, Holt & Fryxell 2009), thereby replacing fat losses incurred during the dry (tropics) or winter (temperate) seasons. Although previous research supports energy maximization as a general foraging strategy for ungulates, the manner in which stopover use facilitates this strategy has yet to be explored.

Our interest here is to evaluate the ecological role of stopovers for temperate ungulates that annually migrate long distances between seasonal ranges, along traditional routes. Ungulates demonstrate strong fidelity to their seasonal ranges (Brown 1992) and migration routes (Berger, Cain & Berger 2006; Sawyer *et al.* 2009), but knowledge of their stopover use and the degree to which stopovers influence migratory patterns and strategies is limited. For example, we do not know how many and what spacing of stopovers are needed to complete migrations, whether ungulates use the same stopovers year after year, and whether stopovers offer better foraging opportunities than other segments of the migration route. Given the relative ease with which fine-scale movement data can be collected with global positioning system-telemetry (GPS), it is now possible to quantify stopover characteristics and examine how stopovers shape the migrations of ungulates and other land migrants.

We used fine-scale movement data collected from GPS collars to examine the ecological role of stopover use for migratory mule deer *Odocoileus hemionus*, where migration distances range from 18 to 144 km. We determined the number of stopovers used during migrations and estimated the number of stopovers needed to complete both spring and autumn migrations as a function of migratory distance. We also examined the spacing of stopovers along the route, calculated the amount of time deer spent in stopovers compared to the movement corridors that connect them and assessed the fidelity of individual animals to stopover sites across seasons and years. We characterized the forage quality of stopovers relative to movement corridors and evaluated whether delayed phenology creates a foraging gradient along the migration route, as commonly assumed in altitudinal migrations (Albon & Langvatn 1992). Finally, we examined whether mule deer used stopovers during time periods when plant phenology was in an early state known to produce high-quality forage. These ecological metrics permit a novel evaluation of stopover use in a temperate ungulate and allow us to assess how stopovers shape the migrations of land migrants that seek to maximize energy intake, rather than speed, during their migrations.

## Materials and methods

We used helicopter net-gunning to capture adult female mule deer across winter ranges in two regions of western Wyoming, USA including: (i) the upper Green River Basin and (ii) the lower Great Divide Basin (LGDB). We fitted deer with store-on-board GPS radio-collars (TGW 3500; Telonics, Inc., Mesa, AZ, USA) programmed to collect one location every 2 or 2.5 h. Collars were programmed to drop off 1–2 years after capture, at which time they were recovered from the field and downloaded. Between 1 December 2005

and 2008, we collected GPS data for 109 migrations (65 spring, 44 autumn) from 68 deer. Detailed information regarding the vegetation and land-use characteristics of the study areas is provided in Sawyer *et al.* (2006, 2009).

### STOPOVER ANALYSIS

We followed the approach of Sawyer *et al.* (2009) to identify migratory stopover sites. First, we used the Brownian bridge movement model (BBMM; Horne *et al.* 2007) to estimate a utilization distribution (UD) for each migration route collected from GPS-collared mule deer (Fig. 1). The BBMM uses time-specific location data to estimate the probability of use along a movement route, where the probability of being in an area is conditioned on the start and end locations, the elapsed time between locations, and the speed of movement (Horne *et al.* 2007). Following UD estimation, stopover sites were classified as the highest 25% quartile in the UD. Such a classification appears to accurately reflect migratory segments where animals actually stop their forward movement, rather than segments where animals move slowly (Sawyer *et al.* 2009; Fig. 1). We used the 'BBMM' package in R (R Foundation for Statistical Computing, Vienna, Austria) to conduct analyses.

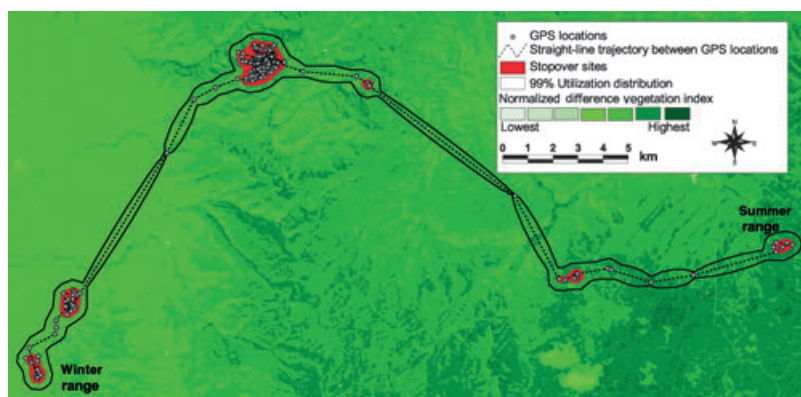
Because the number and spacing of stopovers along a migration route provide key insights into migration strategies, we used linear regression to examine the relationship between migration distance and the number of stopovers. Migration distance was measured along the centreline of each UD estimated for each migration route ( $n = 109$ ). We estimated the number of stopovers used in each deer migration as a function of the total migration distance. Spring ( $n = 65$ ) and autumn ( $n = 44$ ) migrations were analysed separately to account for seasonal differences. To test for non-random spacing of stopovers (i.e. deviation from a linear Poisson process), we measured sojourn distances (Taylor & Karlin 1984), defined as the distance between consecutive stopover sites, for each migration route that had six or more stopovers ( $n = 66$ ). We then compared the observed variance in sojourn distances for each route to the distribution of variances of 5000 simulated routes, upon which the same number of stopovers were randomly placed. We compared the observed variance with the distribution of variances from simulated routes to determine whether stopover location was random, uniform or clumped. Additionally, we characterized the entire distribution of sojourn distances observed in our migration data to evaluate the maximal movement range between stopovers.

We used a paired *t*-test to determine whether the number of stopovers differed between spring and autumn migrations. To control for migration distance, we restricted this analysis to individual deer that had  $> 1$  migration route collected ( $n = 27$ ). We also used a paired analysis to evaluate whether the duration (days) of migration varied between the spring and autumn migrations of individual deer. We characterized the importance of stopover use as the percentage of time each deer spent in stopover habitat while migrating.

The level of fidelity (i.e. repeated use) that deer show to specific stopovers likely reflects the forage benefit of such patches along the route across seasons and years. We examined the fidelity of stopover use across seasons (spring to autumn) by calculating the proportion of stopover sites in the spring migration that overlapped with stopover sites from the subsequent autumn migration. Similarly, we assessed stopover fidelity across years (spring to spring) by calculating the proportion of stopover sites in a spring migration that overlapped with those of the subsequent spring migration. Because these comparisons required paired data, we restricted the seasonal and annual comparisons to mule deer that had at least two (spring and autumn;  $n = 27$ ) or three (spring, autumn, and spring;  $n = 14$ ) observed migration routes, respectively. Additionally, we used an area-based selection ratio approach to determine whether stopover fidelity, from spring to autumn and spring to spring, was more or less than expected by chance. Using stopovers paired within each individual deer, we defined used units as the number of migratory deer locations in one season (e.g. spring 2006) that occurred in the stopover sites of its previous migration (e.g. spring 2005). Because our stopovers were defined as the top 25% of the UD, the expected number of GPS locations to occur in the stopovers of a previous migration was 25% of the total locations. We calculated a selection ratio for each deer and used the 95% CI of the mean ratio among deer to assess whether deer selected stopovers more or less than expected by chance. A selection ratio of 1 indicates no selection (i.e. use is proportional to availability), whereas ratios  $> 1$  indicate selection for and ratios  $< 1$  indicate selection against (Manly *et al.* 2002).

### FORAGE QUALITY ASSESSMENT

The presumed function of stopover sites is to provide foraging habitat during the migration bout, whereas other segments of the migration route function primarily as movement corridors (Sawyer *et al.* 2009). We used the normalized difference vegetation index (NDVI) to determine whether forage quality differed between stopover sites



**Fig. 1.** Six stopover sites and 99% utilization distribution estimated for an individual mule deer (ID no. 10) during spring 2005 migration (32 days) in western Wyoming, USA. Migration route is overlaid on the normalized difference vegetation index calculated during the spring 2005 migration.



and movement corridors. The NDVI is widely used as a measure of forage quality (Hamel *et al.* 2009), primary productivity (Hebblewhite, Merrill & McDermid 2008) and plant phenology (Boone, Thirgood & Hopcraft 2006). Importantly, NDVI is positively correlated with the timing of peak faecal crude protein in temperate ungulates (Hamel *et al.* 2009) and has been successfully used to assess how plant productivity affects their body mass and survival (Pettorelli *et al.* 2007). We restricted our NDVI analysis to mule deer in the LGDB, where open habitats were amenable to remote sensing, and to spring migrations, when imagery was free of snow. Our intent was to obtain a snapshot of NDVI values for the end of the migration period (mid-June), with the expectation that a forage quality gradient associated with elevation should be evident by then. We acquired 30 × 30 m – resolution NDVI data for 14 June 2005 and 14 May 2006 from the US Geological Survey. Reliable imagery from June 2006 was not available because of cloud cover. We randomly selected 15 migration routes from 2005 and 2006 and calculated the average NDVI value in stopovers and movement corridors within each route. The average NDVI value of a movement corridor was calculated from all 30-m cells that intersected the straight lines connecting locations between stopovers. We conducted paired *t*-tests for individual deer to determine whether NDVI values differed between stopovers and movement corridors. To assess whether forage quality varied across the elevation gradient of the migration route, we used the same random sample of 30 deer and regressed the mean NDVI value of each stopover in each year (2005 and 2006) as a function of its mean elevation. In some cases, ungulates may migrate from a low-elevation basin, over a mountain range, and down to another basin destination where elevation is similar to its departure site (e.g. pronghorn *Antilocapra americana*; Berger, Cain & Berger 2006). In this scenario, a forage quality gradient may be associated with elevation, but would not necessarily be positively related to the length of the migration route. To account for this, we also used linear regression to evaluate the relationship between the mean NDVI value of each stopover and its distance from winter range.

#### PHENOLOGICAL TRACKING

The selection of high-quality forage is thought to be the primary mechanism driving ungulate migration (Fryxell & Sinclair 1988), and forage plants are most nutritious to ungulates at the onset of the growing season when they are highly digestible (Albon & Langvatn 1992). In seasonal environments, NDVI can be used to track phenological patterns of vegetation growth, where the seasonal change in 'greenness' can broadly characterize the timing of spring green-up and late-summer or autumn senescence (e.g. Pettorelli *et al.* 2005). For herbivores, access to maximum forage quality presumably occurs prior to the maximum NDVI (i.e. peak green-up), when new vegetation growth steepens the slope of the annual NDVI curve. Indeed, in a study of mountain ungulates, Hamel *et al.* (2009) found the steepest part of the annual NDVI curve was positively correlated with the timing of peak faecal crude protein. Accordingly, we assumed quality forage was most abundant prior to peak green-up, when the NDVI slope was increasing. To assess whether the timing of stopover use corresponded with the phenology of emergent plant growth, we first calculated the mean NDVI value of each stopover for every 8-day period in 2005. We estimated NDVI from 47 MODIS composite images obtained from WYOMINGVIEW (<http://www.uwyo.edu/wy-view>), which had a resolution of 250 m. Using the 47 mean NDVI values in each stopover, we used local polynomial regression function in R (R Foundation for Statistical Computing) to fit a curve and determine the date (Julian day) of the maximum NDVI value within

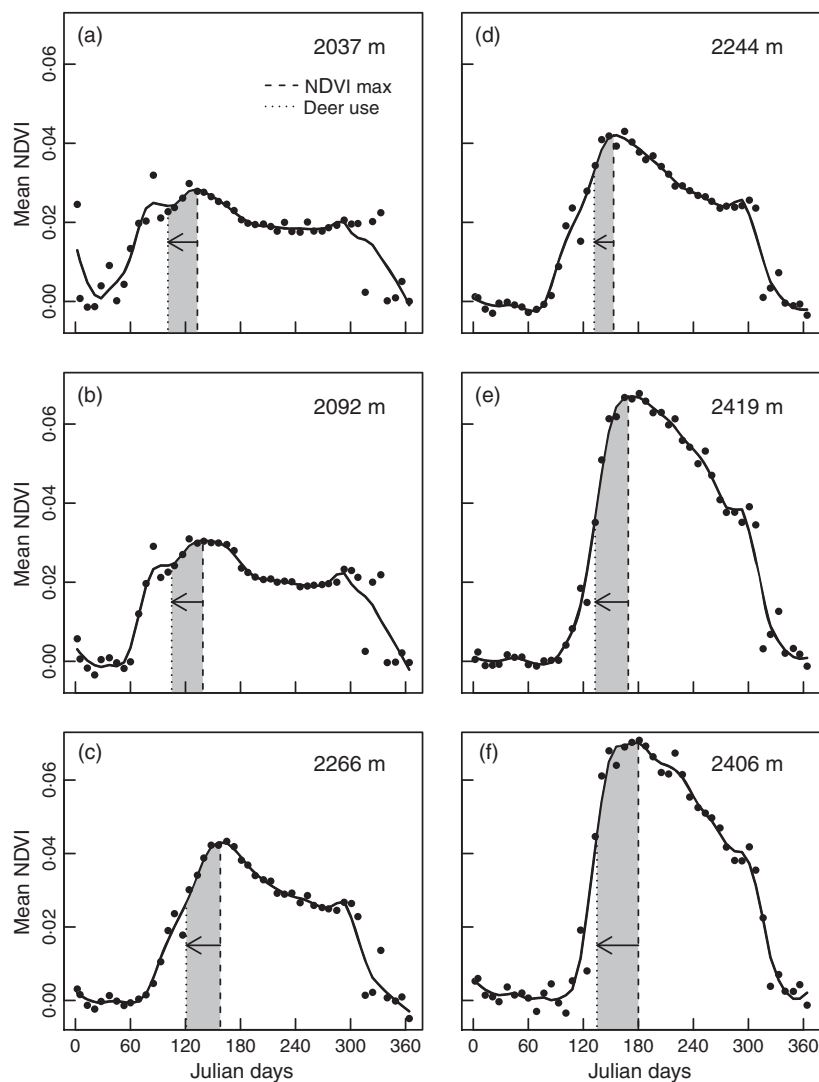
each stopover (Fig. 2). We estimated the timing of stopover use relative to the peak green-up by subtracting the median date of stopover use from the date of maximum NDVI (in Julian days; Fig. 2). After averaging this metric across stopovers for each deer, we then averaged across all deer and reported the mean number of days prior to peak NDVI that deer occupied stopovers. To demonstrate the potential cost of migrating quickly and not using stopovers, we fit the same NDVI curves for the summer ranges of each deer and calculated the phenological stage (Julian days relative to peak NDVI) deer would encounter if they arrived on summer range without stopping over. Because deer can easily travel at rates of 20–50 km day<sup>-1</sup> (Thomas & Irby 1990), we assumed deer could complete migrations in 1 day after leaving winter range. We also estimated the start of green-up based upon the date at which the NDVI curve began to increase (Pettorelli *et al.* 2005). This analysis was restricted to spring because images of stopovers sites used during the autumn migration contained snow-pack. Similar to the sojourn analysis, we restricted this analysis to animals with at least six stopovers ( $n = 18$ ).

#### Results

Regression analysis revealed that the number of stopovers increased significantly with migration distance during both spring ( $F_{1,64} = 696.5$ ,  $P < 0.001$ ,  $R^2 = 0.91$ ) and autumn ( $F_{1,43} = 280.4$ ,  $P < 0.001$ ,  $R^2 = 0.86$ ) migrations (Fig. 3). Estimated coefficients indicated that mule deer used one stopover for every 5.3 and 6.7 km travelled during spring and autumn migrations, respectively. Although the number of stopovers increased linearly with migration distance, the spacing of stopovers was not uniform along the routes. The observed variance in sojourn distances was highly variable, with individual deer showing both uniform and clumped distributions of stopover sites along the route (Fig. 4a). However, the average variance among deer was near the centre of the randomized distributions (mean ± 95% CI, 57 ± 7%) indicating an overall random spacing of stopovers among the population. The distribution of observed sojourn distances indicated that distance between stopovers rarely exceeded 10 km (min = 0.10, max = 25.86, mean = 4.33; Fig. 4b).

Mule deer used more stopovers (mean difference ± 95% CI, 2.07 ± 1.02) in spring migrations compared with autumn ( $t_{26} = 4.03$ ,  $P < 0.001$ ), but the duration (days) of spring (mean ± 95% CI, 21.3 ± 7.6) and autumn (mean ± 95% CI, 20.8 ± 8.5) migrations did not differ ( $t_{26} = 0.13$ ,  $P = 0.896$ ). Across all migrations, mule deer spent 95 ± 0.4% (mean ± 95% CI) of their time in stopovers and only 5% in movement corridors. Deer used the same stopover sites across years, with a higher degree of overlap between the same (spring to spring: 80%,  $n = 14$ , SE = 0.03) vs. different (spring to autumn: 62%,  $n = 27$ , SE = 0.04) seasons ( $t_{37} = -3.43$ ,  $P = 0.001$ ). Selection ratios for spring to spring (mean ± 95% CI, 2.34 ± 0.33) and spring to autumn (mean ± 95% CI, 2.05 ± 0.43) migrations did not overlap 1, indicating strong and consistent selection of stopover sites (i.e. fidelity) between seasons and across years (Fig. 5).

Mean NDVI values were higher in stopovers compared to movement corridors in both 2005 ( $t_{29} = 3.14$ ,  $P = 0.007$ ) and 2006 ( $t_{29} = 3.87$ ,  $P = 0.002$ ), suggesting that forage



**Fig. 2.** Mean normalized difference vegetation index (NDVI) values during stopover use ( $n = 6$ ) by an individual mule deer (ID no. 10). NDVI values were taken every 8 days during 2005, and a smoothed curve was used to determine the date (Julian day) of maximum NDVI representing peak green-up. The median date that the stopover was used by the deer was subtracted from the date of maximum NDVI to characterize the phenological stage of vegetation (i.e. days prior to peak green-up; shaded area) for the time period of stopover use. Panels (a) through (f) correspond to stopovers depicted in Fig. 1 and progress from winter range (a) to summer range (f). On average, deer occupied stopovers  $44 \pm 6$  days (mean  $\pm$  SD) before peak green-up. The mean elevation of the stopover is noted in the top right corner of each panel.

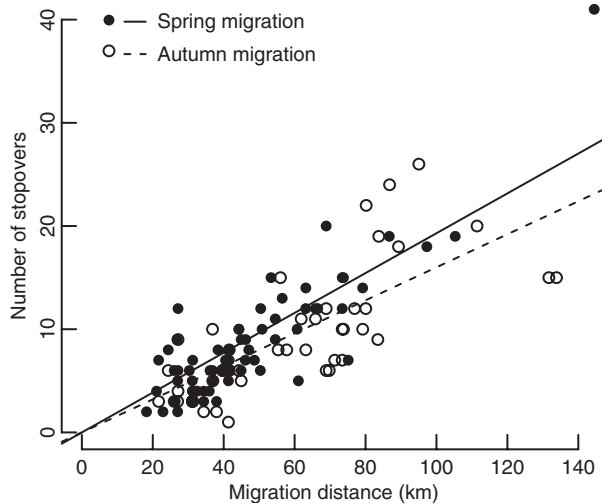
quality was higher in stopovers than in movement corridors (Fig. 6). The mean NDVI value of stopovers was higher in 2005 compared with 2006 because the imagery was obtained 30 days later in the spring. Regression analysis revealed that NDVI values of stopovers increased with elevation (2005;  $P < 0.001$ ,  $F_{1,110} = 150.5$ , and 2006;  $P < 0.001$ ,  $F_{1,115} = 72.8$ ) and distance from winter range (2005;  $P < 0.001$ ,  $F_{1,110} = 60.8$ , and 2006;  $P < 0.001$ ,  $F_{1,115} = 10.6$ ) in both years (Fig. 7).

During spring migration, stopover use consistently occurred  $44 \pm 6$  days (mean  $\pm$  SD) before peak green-up (Fig. 8), suggesting that the timing of stopover use was tied to phenological changes along the elevational migrations. In contrast, had deer not used stopovers and simply migrated directly to summer range, their arrival on summer range would have been  $75 \pm 19$  days (mean  $\pm$  SD) prior to peak green-up. The use of stopovers 44 days prior to peak green-up was a remarkably consistent response across individual animals ( $n = 18$ ) and led us to conclude that this was the optimal time period for deer to exploit high-quality forage. Using this optimal time period, we then asked what pheno-

logical stage deer would experience on winter range if they waited there and only migrated (without stopping over) once their summer range was within 44 days of peak green-up. Under this strategy, deer would experience forage quality associated with the plant community at  $3 \pm 17$  days (mean  $\pm$  SD) days prior to peak green-up. We do not have field data to characterize the relationship between plant nutrition and phenological stage of seasonal habitat, but given that green-up started  $97 \pm 7$  days (mean  $\pm$  SD) prior to peak green-up, we assume that forage quality is likely to be suboptimal shortly after the start of green-up and at the peak, when plants are beginning to senesce (Fig. 8).

## Discussion

Our findings suggest that the ecological benefits of stopovers are not limited to avian taxa. Rather, we show that stopovers also play a critical role in the altitudinal migrations of temperate ungulates that maximize energy intake, rather than speed, during migration. Mule deer utilized a series of stopover sites along their seasonal migrations routes, to which



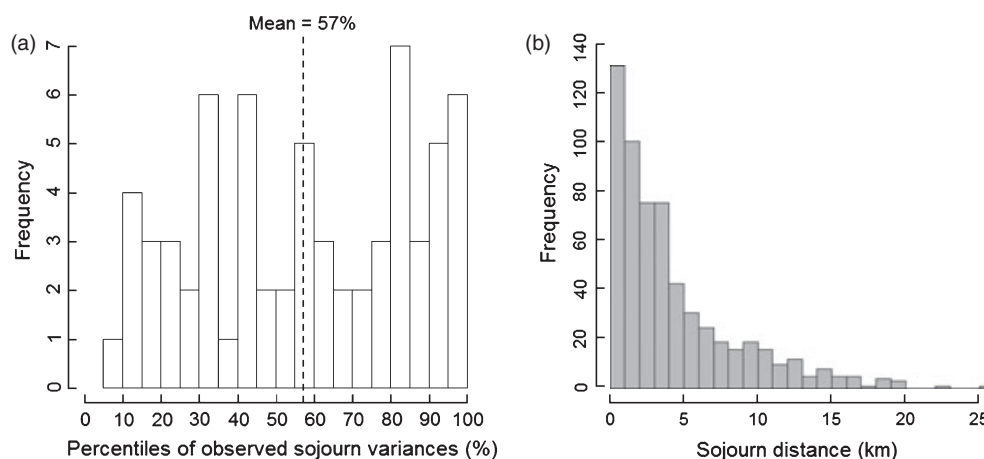
**Fig. 3.** The number of stopovers used by mule deer increased with migration distance (km) during spring ( $n = 65$ ; filled circles;  $P < 0.001$ ) and autumn ( $n = 44$ ; open circles;  $P < 0.001$ ) migrations. On average, deer used one stopover for every 5.3 and 6.7 km travelled during spring and autumn migrations, respectively.

they had high annual fidelity. Deer spent 95% of their migration time in stopovers, and the number of stopovers increased linearly with migration distance. Our NDVI analysis indicated that stopovers had higher forage quality compared to the movement corridors that connect them, and that the forage quality of stopovers increased with elevation and distance from winter range. Additionally, our temporal NDVI analysis suggested that deer used stopovers in the spring to track phenological changes in vegetation, such that they occupied stopovers only during the period of emergent vegetation growth, prior to peak green-up. Stopovers are known to play a key role in the migration ecology of avian taxa (Alerstam &

Hedenström 1998; Newton 2008), and our results suggest they may be equally important to land migrants, such as temperate ungulates.

Across a wide range of migratory distances (18–144 km), the number of stopovers increased linearly with migration distance, with deer using one stopover every *c.* 5–7 km along the migration route. While these results indicate a reliance on stopovers throughout the migratory bout, sojourn analysis indicated that the spacing of stopovers along migration routes was not uniform. This suggests that deer require stopovers while migrating, but were not severely constrained by stopover spacing and were able to use both shorter and longer distances between stopovers. We suspect that the range (*c.* 0–10 km) and random spacing of sojourn distances is a result of mule deer optimizing their stopover use in a landscape of heterogeneous foraging opportunities. Further research is needed to determine the degree to which variable sojourn distances allow land migrants such as temperate ungulates to establish and maintain migration routes in heterogeneous (and changing) landscapes. Because the energetic constraints of movement are strongly influenced by body size (Alexander 1998; Alerstam, Hedenström & Åkesson 2003), the sojourn abilities of larger-bodied land migrants (e.g. elk) may be more plastic than deer.

Mule deer utilized a series of stopover sites along their migration routes, but tended to use more stopovers in spring than in autumn. Seasonal differences in stopover use did not result from variable rates of travel, but they may have been influenced by deer shifting their diets from primarily herbaceous forage in the spring to woody browse in the autumn. We hypothesize that differential use of stopovers between seasons allows deer to accommodate different environmental conditions and optimize their foraging patterns, without having to navigate different pathways in the spring and autumn. Birds, for example, often encounter different envi-



**Fig. 4.** (a) The placement (percentile) of the observed sojourn variances ( $n = 66$ ) within the distribution of variances from simulated routes indicates random or non-random placement of stopovers: low percentile values ( $< 5\%$ ) indicate uniform spacing, while high values ( $> 95\%$ ) indicate clumped spacing. The average variance near the centre (57%) of the randomized distributions indicates an overall random spacing of stopovers among the population. (b) Histogram of sojourn distances measured from mule deer migration routes in western Wyoming, USA, indicates that sojourn distances rarely exceed 10 km.

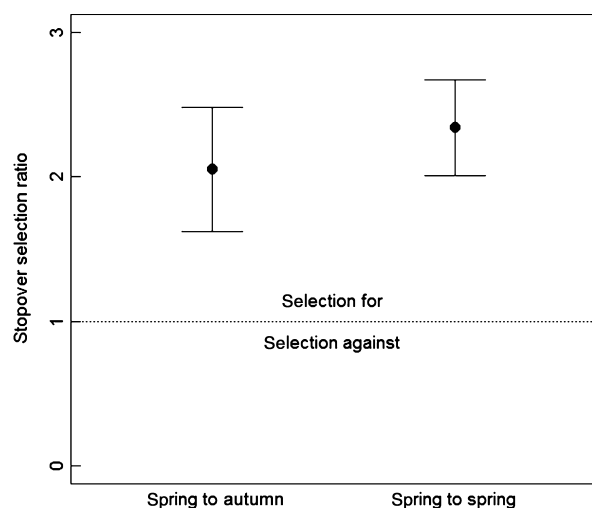


Fig. 5. Mule deer had high annual fidelity to their stopover sites as evaluated by selection ratios and 95% CIs calculated for spring to spring and spring to autumn stopover sites. A selection ratio  $> 1$  indicates deer selection for stopover sites was greater than expected by chance.

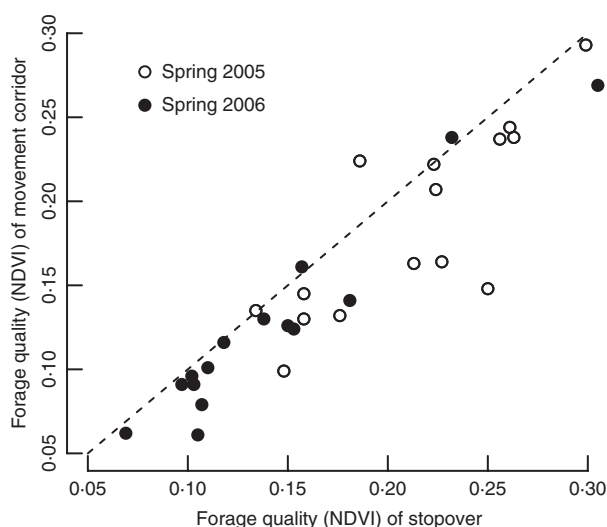


Fig. 6. Average normalized difference vegetation index values in movement corridors and stopovers of mule deer migration routes in spring 2005 ( $n = 15$ ; open circles) and 2006 ( $n = 15$ ; solid circles), in western Wyoming, USA. Diagonal line represents 1 : 1 relationship between forage quality of paired stopovers and movement corridors. Deer selected stopovers that had higher forage quality than route segments used as movement corridors in 2005 ( $P < 0.007$ ) and 2006 ( $P < 0.002$ ).

ronmental conditions (e.g. prevailing winds) during spring and autumn migrations, which they can behaviourally mediate by completing loop migrations, i.e. a migratory pattern where the autumn migration route is markedly different from the spring (Newton 2008).

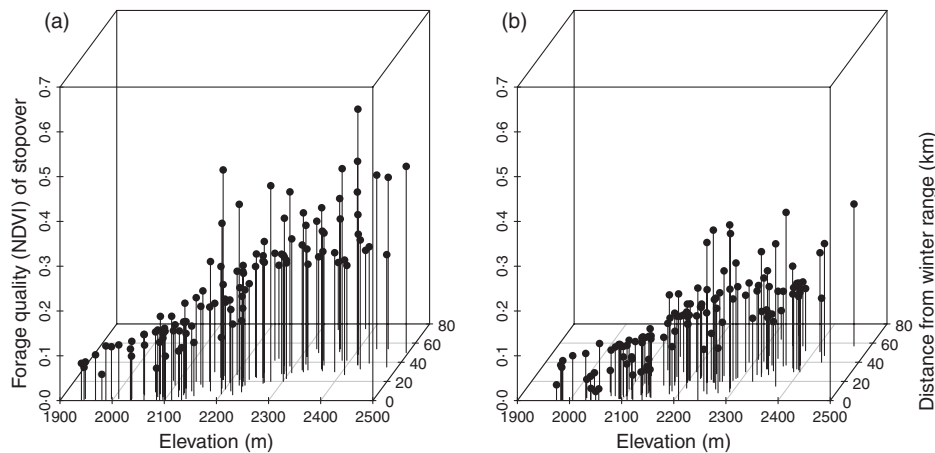
An implicit assumption of stopovers is that they provide better foraging opportunities than other segments of the migration route. Our analysis showed that forage quality, as indexed by NDVI, was higher in stopovers compared to

movement corridors. This finding suggests that selection of stopovers is influenced by forage quality, and similar to birds (Alerstam, Hake & Kjellen 2006), the fidelity analysis showed that deer return to these same areas in spring and autumn migrations of subsequent years. Temporal patterns of NDVI have been found to be related to ungulate growth and survival (Pettorelli *et al.* 2007), and temperate ungulates are known to select habitat patches with high NDVI during the growing season (Thomas, Johnson & Griffith 2006; Hebblewhite, Merrill & McDermid 2008). Although other factors such as predation risk may also affect stopover selection in birds (Lindström 1990; Pomeroy, Butler & Ydenberg 2006), our findings of frequent and consistent stopover use, coupled with higher forage quality in stopover patches, provide evidence of the foraging benefit of stopover use in this migratory deer population.

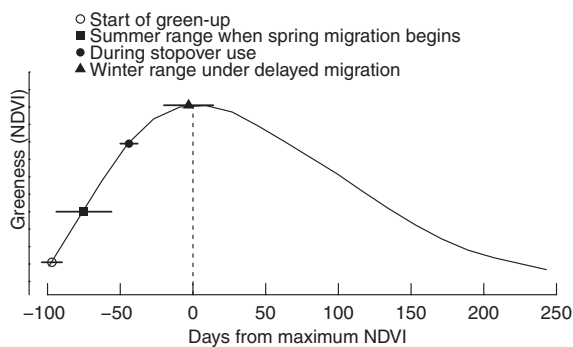
An assumption of altitudinal migration is that delayed phenology associated with elevation creates a nutritional gradient, where the phenology of vegetation is delayed at higher elevations and provides higher forage quality compared to lower elevations (Albon & Langvatn 1992). In a recent study of a partially migratory elk herd, Hebblewhite, Merrill & McDermid (2008) found that delayed phenology allowed migratory animals to improve their forage quality 6.5% over non-migrants by accessing vegetation at higher elevations. Similarly, Albon & Langvatn (1992) found that crude protein was positively correlated with elevation, and that body weights of red deer (*C. elaphus*) that migrated to higher elevations were higher than those that did not. We found that forage quality of stopovers was positively correlated with elevation and distance from winter range. Temporally, forage quality for such altitudinal migrations may best be viewed as a phenological wave that advances from lower to higher elevation. Indeed, the ability of migratory ungulates to exploit such gradients in forage quality is a key benefit to their migratory life history (Fryxell & Sinclair 1988). If ungulate migration is driven by the selection of high-quality forage, then the duration of altitudinal migrations should correspond with the delayed phenology associated with elevation gradients. For example, given a phenology delay of 50 days for every 1000-m increase in elevation (Hebblewhite, Merrill & McDermid 2008), we would expect a 420-m elevation gain in the average 21-day migration period observed in our study. Consistent with this prediction, the average elevation gain for migrating deer was  $324 \pm 60$  m (mean  $\pm$  95% CI). These findings suggest that stopover use in temperate ungulates is a behavioural mechanism that allows individuals to exploit forage quality gradients created by phenological delays associated with elevation.

The movement rates of deer support the notion that they use stopovers to exploit phenological gradients. We know ungulates are capable of moving long distances in short periods of time ( $20\text{--}50$  km day $^{-1}$ ; Thomas & Irby 1990; Berger, Cain & Berger 2006), yet deer migrations we observed took 3 weeks to complete. This slow rate of migration, combined with routine stopover use, is consistent with a migration strategy designed to exploit nutritional gradients. If a





**Fig. 7.** Mean normalized difference vegetation index value of stopovers used by 15 mule deer migrating in western Wyoming, USA, plotted as a function of mean elevation (m) and distance from winter range (km) in 2005 (a) and 2006 (b). Forage quality of stopovers increased with elevation ( $P < 0.001$ ) and distance ( $P < 0.001$ ) from winter range in both years because of phenological delays associated with elevation and topography.



**Fig. 8.** Deer utilized stopovers 44 days prior to peak green-up (●), when vegetation greenness was increasing and access to quality forage was assumed to be maximized. Had deer migrated directly to summer range without using stopovers, they would arrive 75 days prior to peak green-up (■), shortly after vegetation growth begins (○) and likely have to wait several weeks for quality forage conditions to be realized. Assuming that 44 days prior to green-up is the optimal time to arrive on summer range, and that deer choose to wait on winter range and then migrate directly to summer range, they would be required to stay on winter range through peak green-up (▲, delayed migration), when vegetation begins to senesce. Data are overlaid on a conceptualized greenness curve and error bars represent  $\pm 1$  SD.

phenology gradient did not exist along the migration route, we would expect ungulates to either complete their migrations more quickly without using stopovers or possibly not migrate. Our phenological tracking analysis showed that deer used stopovers 44 days prior to peak green-up, when vegetation greenness was increasing and forage quality assumed to be the highest. Had deer not used stopovers and simply migrated directly to their summer ranges, they would arrive 75 days prior to peak green-up and have to wait several weeks for optimal foraging conditions, as indexed by the steepness of the annual NDVI curve. Temperate ungulates rely on summer foraging to meet the energetic costs of lactation and accumulate fat reserves necessary to survive the

following winter (Cook *et al.* 2004; Parker, Barboza & Gillingham 2009). Overall, stopover use appears to facilitate a strategy that effectively reduces the amount of time spent on winter range, allowing individuals to recover body condition earlier in the spring and maintain it longer in the autumn. Thus, unlike birds that utilize stopovers to speed up their migrations by optimizing fuel loads (Hedenström 2008), ungulates appear to use stopovers to slow down, allowing them to migrate in concert with plant phenology and maximize energy intake along the route.

The conservation of stopover habitat has become a clear goal of agencies and non-governmental organizations tasked with sustaining migratory bird populations (Mehlman *et al.* 2005). Assuming that stopovers play a critical role in the annual energy budgets of mule deer, and given the strong fidelity that deer showed to stopovers across seasons and years, the protection of stopover sites may provide an effective conservation strategy for migratory ungulates as well. A relatively new, but potentially important consideration with the conservation of migratory species in seasonal environments is whether the timing of their migrations can match the phenological peaks of food abundance that may change because of warming climate (Visser & Both 2005). When migratory species cannot adjust the timing of their movements with climate-induced changes in food abundance, the resulting phenological or trophic mismatch (Stenseth & Mysterud 2002) can have fitness consequences (Both *et al.* 2006). Compared to ungulates, birds are more susceptible to trophic mismatches because their migrations are often initiated from cues (e.g. photoperiod) that may not provide reliable information on the phenological conditions of the destination site. In contrast, the migrations of temperate ungulates are cued by forage conditions (Garrott *et al.* 1987; Albon & Langvatn 1992), and the consistent use of stopovers along the migration route may provide them with the information needed to track phenological conditions and adjust the timing of their migrations, such that trophic mismatches associ-



ated with climate change (e.g. Post *et al.* 2008) are avoided. Indeed, our phenological tracking suggests that deer can adjust the timing of their stopover use to correspond with phenological progression, and thus the variation in forage quality, associated with elevation gradients.

A common denominator among migratory taxa is the use of stopovers. For birds, stopover use allows them to minimize migration time and energy cost by migrating in short steps with small fuel loads, rather than long steps with large fuel loads (Alerstam & Hedenström 1998). Our work on mule deer provides the first empirical evaluation of the ecological role of stopovers for a land migrant. Similar to birds, deer migrations were characterized by relatively short movement steps interrupted by stopover sites that had higher forage quality than the adjoining movement corridors. Although deer could have completed migrations in a number of days, they instead took an average of 3 weeks to complete and spent 95% of that time in stopovers. These findings suggest that the general foraging strategy of ungulates to maximize energy intake is facilitated by stopover use during migration, where stopover use allows individuals to migrate in step with vegetation phenology. Our work suggests that stopover use may be more common among non-avian taxa than previously thought and, although the underlying migration strategies of temperate ungulates and birds are quite different, stopover use is important to both. Exploring the role of stopovers in land migrants broadens the scope of stopover ecology and recognizes that the applied and theoretical benefits of stopover ecology need not be limited to avian taxa.

## Acknowledgements

We thank R.M. Nielson and T.L. McDonald for statistical consultation and S. Lanning and R. Klaver for image processing. D. Doak, S. Buskirk, A. Middleton, C. McCarthy and N. Korfanta helped refine earlier drafts of the manuscript. Further input from T. Coulson, M. Wunder and J. Fryxell improved the manuscript considerably. This work was supported by the University of Wyoming's School of Energy Resources, the Wildlife Heritage Foundation of Wyoming, the US Geological Survey's Wyoming Landscape Conservation Initiative, and grants provided to Western Ecosystems Technology, Inc from Anadarko Petroleum Company, the Bureau of Land Management, and Questar Exploration and Production. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

## References

- Åkesson, S. & Hedenström, A. (2007) How migrants get there: migratory performance and orientation. *BioScience*, **57**, 123–133.
- Albon, S.D. & Langvatn, R. (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, **65**, 502–513.
- Alerstam, T., Hake, M. & Kjellen, N. (2006) Temporal and spatial patterns of repeated journeys by ospreys: implications for strategies and navigation in bird migration. *Animal Behaviour*, **71**, 555–566.
- Alerstam, T. & Hedenström, A. (1998) The development of bird migration theory. *Journal of Avian Biology*, **29**, 343–369.
- Alerstam, T., Hedenström, A. & Åkesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.
- Alexander, R.McN. (1998) When is migration worthwhile for animals that walk, swim or fly? *Journal of Avian Biology*, **29**, 387–394.
- Berger, J., Cain, S.L. & Berger, K.M. (2006) Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters*, **22**, 528–531.
- Bishop, C.J., White, G.C., Freddy, D.J., Watkins, B.E. & Stephenson, T.R. (2009) Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs*, **172**, 1–28.
- Boone, R.B., Thirgood, S.J. & Hopcraft, J.G.C. (2006) Serengeti wildebeest migratory patterns modeled from rainautumn and new vegetation growth. *Ecology*, **87**, 1987–1994.
- Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in long-distance migratory bird. *Nature*, **441**, 81–83.
- Brown, C.G. (1992) Movement and migration patterns of mule deer in south-eastern Idaho. *Journal of Wildlife Management*, **56**, 246–253.
- Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. & Irwin, L.L. (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.
- Dingle, H. & Drake, V.A. (2007) What is migration? *BioScience*, **57**, 113–121.
- Erni, B., Liechti, F. & Bruderer, B. (2002) Stopover strategies in passerine bird migration: a simulation study. *Journal of Theoretical Biology*, **219**, 479–493.
- Franke, A., Caelli, T. & Hudson, R.J. (2004) Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models. *Ecological Modelling*, **173**, 259–270.
- Fryxell, J.M. (1991) Forage quality and aggregation by large herbivores. *The American Naturalist*, **138**, 478–498.
- Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, **3**, 237–241.
- Fryxell, J.M., Wilmschurst, J.F. & Sinclair, A.R.E. (2004) Predictive models of movement by Serengeti grazers. *Ecology*, **85**, 2429–2435.
- Garrott, R.A., White, G.C., Bartmann, R.M., Carpenter, L.H. & Alldredge, A.W. (1987) Movements of female mule deer in northwest Colorado. *Journal of Wildlife Management*, **51**, 634–643.
- Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J.-M. & Côté, S.D. (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *Journal of Applied Ecology*, **46**, 582–589.
- Hebblewhite, M., Merrill, E.H. & McDermid, G. (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, **78**, 141–166.
- Hedenström, A. (2003a) Optimal migration strategies in animals that run: a range equation and its consequences. *Animal Behaviour*, **66**, 631–636.
- Hedenström, A. (2003b) Scaling migration speed in animals that run, swim, and fly. *Journal of Zoology*, **259**, 155–160.
- Hedenström, A. (2008) Adaptations to migration in birds: behavioural strategies, morphology, and scaling effects. *Philosophical Transactions of the Royal Society B*, **363**, 287–299.
- Hobbs, N.T. (1989) Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs*, **101**, 1–39.
- Holdo, R.M., Holt, R.D. & Fryxell, J.M. (2009) Opposing rainautumn and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**, 43–445.
- Horne, J.S., Garton, E.O., Krone, S.M. & Lewis, J.S. (2007) Analyzing animal movements using Brownian Bridges. *Ecology*, **88**, 2354–2363.
- Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002) Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, **71**, 225–235.
- Lindström, A. (1990) The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behavioral Ecology*, **1**, 102–106.
- Manly, B.F., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd edn. Kluwer Academic Publishers, Boston.
- McNaughton, S. J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 260–294.
- Mehlman, D.W., Mabey, S.E., Ewert, D.N., Duncan, C., Abel, B., Cimprich, D., Sutter, R.D. & Moodrey, M. (2005) Conserving stopover sites for forest-dwelling migratory landbirds. *Auk*, **122**, 1281–1290.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.
- Newton, I. (2008) *The Migration Ecology of Birds*. Elsevier Ltd., San Diego.
- Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009) Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.
- Parker, K.L., Robbins, C.T. & Hanley, T.A. (1984) Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management*, **48**, 474–488.

- Pettorelli, N., Pelletier, F., Hardenberg, A.V., Festa-Bianchet, M. & Côté, S.D. (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology*, **88**, 381–390.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503–510.
- Pomeroy, A.C., Butler, R.W. & Ydenberg, R.C. (2006) Experimental evidence that migrants adjust usage at stopover site to trade off food and danger. *Behavioral Ecology*, **17**, 1041–1045.
- Post, E., Pedersen, C., Wilms, C.C. & Forchhammer, M.C. (2008) Warming, plant phenology and the dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society B*, **275**, 2005–2013.
- Ramenofsky, M. & Wingfield, J.M. (2007) Regulation of migration. *BioScience*, **57**, 138–143.
- Sawyer, H., Nielson, R.M., Lindzey, F. & McDonald, L.L. (2006) Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management*, **70**, 396–403.
- Sawyer, H., Kauffman, M.J., Nielson, R.N. & Horne, J.S. (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, **19**, 2016–2025.
- Stenseth, N.C. & Mysterud, A. (2002) Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences (USA)*, **99**, 13379–13381.
- Taylor, H.M. & Karlin, S. (1984) *An Introduction to Stochastic Modeling*. Academic Press, London.
- Thomas, T. & Irby, L. (1990) Habitat use and movement patterns by migrating mule deer in southeastern Idaho. *Northwest Science*, **64**, 19–27.
- Thomas, D.L., Johnson, D. & Griffith, B. (2006) A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. *Journal of Wildlife Management*, **70**, 404–412.
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B*, **272**, 2561–2569.
- Weber, T.P. & Houston, A.I. (1997) Flight costs, flight range and the stopover ecology of migrating birds. *Journal of Animal Ecology*, **66**, 297–306.
- Wilms, J. F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999) Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, **77**, 1223–1232.

Received 2 August 2010; accepted 18 March 2011

Handling Editor: Mike Wunder