

## Factors driving variation in movement rate and seasonality of sympatric ungulates

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Defining biologically relevant seasons is a critical issue in the interpretation of animal space-use studies. Moreover, understanding the effects of extrinsic (e.g., predation risk) and intrinsic (e.g., age and sex) factors on individual differences in seasonal transition dates will deepen our understanding of the mechanisms driving animal movement and potentially population dynamics. We used nonlinear modeling of movement rate over time using global positioning system-collared nonmigratory elk (*Cervus elaphus manitobensis*) and white-tailed deer (*Odocoileus virginianus*) in southern Manitoba, Canada, to derive species- and sex-specific seasonal transition dates. In addition, we used variables known to influence timing of migration in migratory populations to explain individual differences in seasonal transition dates. We found ecologically important differences in start and length of seasons between male and female elk and white-tailed deer. Individual differences in seasonal transition dates were large, and could be explained by a combination of intrinsic and extrinsic factors. Age-class of the individual animal and elevation influenced timing of winter, spring, and date of parturition, whereas predation risk from wolves (*Canis lupus*) influenced onset of spring, summer, and autumn. Our findings suggest that similar extrinsic and intrinsic factors can influence both large- (i.e., migratory) and small-scale movement patterns and can be used effectively to empirically define biologically relevant seasons for sympatric large herbivores.

Key words: birth synchronization, fitness, movement, nonlinear modeling, predation risk, sympatric ungulates, temperature

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The ecological importance of animal movement is apparent by its growing application in both foraging (Owen-Smith et al. 2010) and habitat-selection (de Jager et al. 2011; Martin et al. 2008) theory. Defining biologically relevant seasons is critical in the interpretation of animal space-use patterns (Börger et al. 2006) and to identify species interactions (Basille et al. 2012), which underlines the need for objective procedures to derive population-level seasonal transition dates. Recent studies have shown that modeling movement rate over time is an effective approach to empirically define seasonality for several large herbivore populations such as woodland caribou (*Rangifer tarandus caribou*—Basille et al. 2012; Ferguson and Elkie 2004), moose (*Alces alces*—Basille et al. 2012; Vander Wal and Rodgers 2009), and elephants (*Loxodonta africana*—Birkett et al. 2012). However, evaluating individual differences in seasonal transition dates and the effect of extrinsic (e.g.,

predation risk) or intrinsic (e.g., age and sex) factors remain unexplored despite its potential importance to link spatial and temporal variation in animal movement behavior to individual fitness and population dynamics (Morales et al. 2010; Nicholson et al. 1997).

Delineation of seasons in animal space-use studies has typically ignored the basic ecology of the species and has been done by following calendar dates (Beier and McCullough 1990), although often no criteria are used at all. Alternative approaches to define seasonality have used environmental proxies such as snow depth (Fieberg et al. 2008) or plant phenology (Bjørneraas et al. 2011). However, variation in



environmental conditions over space and time combined with an animal's intrinsic state may confound such classification and a less subjective, more empirical method is needed to derive seasonality directly from the data (Basille et al. 2012; Vander Wal and Rodgers 2009). Identifying seasons based on movement rate of hibernating or migrating species is relatively straightforward, because abrupt changes in movement rate can be observed between start and end of such life-history stages (Bunnefeld et al. 2011; Nelson et al. 2004). More challenging, however, is delineating seasonality of nonmigratory animals, especially because movement rates are often highly variable among individuals and the response is measured on a much smaller spatial scale (Mueller et al. 2011).

The aims of our study were to develop and evaluate an analytical framework based on generalized additive mixed models to define species- and sex-dependent seasonality by quantifying temporal changes in movement rate of sympatric, nonmigratory prairie-parkland elk (*Cervus elaphus manitobensis*) and white-tailed deer (*Odocoileus virginianus*); and to assess the effect of multiple extrinsic and intrinsic variables on individual differences in seasonal transition dates. Previous analyses of elk and white-tailed deer movement patterns in North America have shown that movement rates change in response to local weather (Beier and McCullough 1990; Parker et al. 1984; Webb et al. 2010) and forage variability (Ager et al. 2003; Wickstrom et al. 1984), which reflect fine-scale behavioral strategies to alleviate thermal constraints and to optimize foraging opportunities (van Beest et al. 2011). Indeed, movement rate of white-tailed deer is negatively related to cold ambient temperatures during winter, whereas the reverse, low movement rates at high temperature, is evident during summer (Webb et al. 2010). Similar nonlinear patterns in movement rate of elk have been observed during periods of forage green-up and forage maturation (Wickstrom et al. 1984). In some instances, however, a clear association between movement patterns and environmental conditions is absent and instead life-cycle stages (e.g., rutting and parturition) and associated activity patterns may be better suited to define seasonality (Beier and McCullough 1990; Bowyer 1981; Brook 2010; Dzialak et al. 2011).

Movement rate of individuals changes in response to multiple extrinsic and intrinsic conditions. As such, analysis of movement rate integrates expected (a priori) as well as unexpected factors that influence animal behavior (Vander Wal and Rodgers 2009). However, if our movement-based approach is effective in delineating ecologically meaningful seasons, at least a part of the observed variation in season-specific movement rate should be related to environmental conditions observed in the field (Birkett et al. 2012). To evaluate and test our model we developed a series of a priori predictions regarding the direction of season-specific movement rate and its relation to either ambient temperature or growing degree days (GDD), which can be used as a proxy for forage green-up and productivity (McMaster and Wilhelm 1997; Rivrud et al. 2010). During winter, we expected movement rate for both species and sexes to decrease and to

be positively related to ambient temperature (prediction 1a [ $P_{1a}$ ]). During spring we expected movement rate to increase and to be positively associated to GDD ( $P_{1b}$ ). During summer we expected movement rate to decrease and to be negatively correlated to ambient temperature ( $P_{1c}$ ). In addition, we expected a short-term decrease followed by a steady increase in movement rate during summer for females to reflect calving period ( $P_{1d}$ ). Similarly, we expected movement rate during autumn to increase and to peak during the pinnacle of the rutting or breeding season ( $P_{1e}$ ).

Movement patterns of both migratory and nonmigratory species are believed to be aimed at maximizing individual fitness (Boyce 1991). Individual and environmental drivers known to affect timing of migration may, therefore, provide a useful basis to understand individual differences in seasonality of nonmigratory species. For example, fluctuating forage resources over altitudinal ranges and spatial variation in predation risk typically initiate seasonal migration of large herbivores (Fryxell and Sinclair 1988; Mysterud 1999). In addition, migration status and timing may differ according to age and sex (White et al. 2010). Such extrinsic and intrinsic influences are equally likely to affect individual differences in seasonality of nonmigratory species, although this remains untested. We expected individual differences in seasonal transition dates to be influenced by topography, predation risk by wolves, age, year, sex, and species ( $P_2$ ) because these factors have previously been demonstrated to influence timing of migratory behavior of elk (Hebblewhite and Merrill 2009; White et al. 2010) and white-tailed deer (Grovenburg et al. 2011).

## MATERIALS AND METHODS

*Study area.*—The study area (see Supporting Information S1, DOI: 10.1644/080.S1) is located in the Prairie and Boreal Plain ecozones in southwestern Manitoba, Canada. Most of the area outside of protected areas is currently managed for intensive agriculture, primarily the production of annual cereal and oilseed, as well as perennial forage crops, and pasture for beef cattle (Brook 2010). The area includes Riding Mountain National Park, a relatively undisturbed, largely forested area of 2,974 km<sup>2</sup> (50°51'N, 100°15'W). Winter surveys have indicated a stable wolf population (~80 individuals) present in the area since 1976 (Stronen et al. 2012). Elk and white-tailed deer are the dominant food sources for wolves in this area (Paquet 1992).

*Global positioning system data.*—Between 2003 and 2011, a total of 36 elk ( $n = 12$  males,  $n = 24$  females) and 20 white-tailed deer ( $n = 11$  males,  $n = 9$  females) were captured with a net-gun fired from a helicopter (Brook 2010). All animal capture and handling was conducted in accordance with the guidelines of the Canadian Council on Animal Care, protocol F01-037, and the Canadian Environmental Assessment Registry Reference 03-01-473, and complied with guidelines published by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011). Each animal

was fitted with a global positioning system (GPS) collar programmed with a 2-h relocation schedule for up to 1 year. Spatial errors associated with the GPS collars ( $\bar{X} \pm SE = 14 \pm 17$  m) determined by placing the collars at fixed locations for several days were considered small enough not to bias the movement analyses (Johnson and Gillingham 2008). All GPS locations were screened for large positional outliers. Outliers were defined as locations where movement between 2 successive GPS locations exceeded 30 km/h and the angle of the erroneous location was greater than  $166^\circ$  but less than  $194^\circ$  (i.e., the animal is returning in roughly the same direction it came from). With this approach we removed 2,487 (1,643 for elk and 844 for white-tailed deer) erroneous locations ( $<2\%$  of the full GPS data set). GPS positions collected within 24 h of capture also were excluded, which is typically done when assessing fine-scale animal movements (van Beest et al. 2011). Because we were interested in modeling movement rate over time we selected only individuals with a complete 1-year GPS data set and with at least 8 GPS locations/day to make sure that all individuals provided equal weight to the analysis. These criteria reduced the final sample size to 18 elk ( $n = 7$  males,  $n = 11$  females) and 9 white-tailed deer ( $n = 6$  males,  $n = 3$  females).

*Modeling population-level seasonality.*—We expected movement rate to change between seasons. However, an increase or decrease in movement rate (m/h) of large herbivores also can be observed within seasons, especially following a short-term disturbance event related to human activity (Reimers et al. 2003; Stoen et al. 2010). Such changes in movement rate are typically of short duration (e.g., hours—Stoen et al. 2010). To avoid potential bias due to such atypical movements we calculated daily movement rates ( $m\ h^{-1}\ day^{-1}$ ) for each GPS-collared individual separately, using the library *adehabitat* implemented in R (R Development Core Team 2012). To parameterize seasonal response curves depicting daily movement rates of elk and white-tailed deer during the year we used generalized additive mixed models in the R library *mgcv*. We expected movement rate of elk and white-tailed deer to change nonlinearly over time and a decrease or increase in movement rate (i.e., inflection points) to delineate the start or end of a season (Dzialak et al. 2011; Vander Wal and Rodgers 2009). Generalized additive mixed models provide a suitable framework to model such changes in movement because explanatory variables, with expected nonlinear effects, can be fitted as parametric or nonparametric smoothing terms (Wood 2006). Moreover, variables can be modeled as random effects and any residual dependence among observations can be modeled using correlation structures (Pinheiro and Bates 2000; Wood 2006). Log-transformed movement rate ( $m\ h^{-1}\ day^{-1}$ ) was fitted as the response variable. Julian day was included as a smoothing function for each species and sex separately. We used cyclic regression splines, with the optimal smooth curve estimated by the generalized cross-validation procedure (Wood 2006). To account for repeated measurements from the same individual (ID), animal ID was fitted as a random intercept. Any temporal

dependence among observations was modeled using a rational quadratic correlation structure (*corRatio*) because this provided the best fit based on Akiake's information criterion (Pinheiro and Bates 2000). Species, sex, and their interaction were fitted as additional explanatory variables. Post hoc paired Tukey's honestly significant difference tests were performed to determine where differences in mean movement rate between species and sex occurred. Year did not significantly affect movement rate over time for any of the species or sexes considered and was not included in the population-level model. To identify population-level seasonal transition dates we used model predictions of the generalized additive mixed model analysis to calculate, for each sex and species separately, the date of each inflection point (i.e., day with a significant change [increase or decrease] in movement rate).

*Evaluating the population-level seasonality model.*—To evaluate the effectiveness of our population-level model to identify ecologically meaningful seasons we tested for correlations (Pearson  $r$ ) between seasonal specific movement rate (for each species and sex separately) and daily ambient temperature and GDD. Data on daily temperature (minimum, mean, and maximum) available for the whole study period was taken from the closest meteorological station (approximately 20 km from the center of the study area; <http://www.weatheroffice.gc.ca>). Following McMaster and Wilhelm (1997), GDD was calculated using the formula:

$$GDD = \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}},$$

where  $T_{\max}$  is the daily maximum air temperature,  $T_{\min}$  is the daily minimum air temperature, and  $T_{\text{base}}$  is the base temperature, which was set to  $5^\circ\text{C}$  because this is considered to be the minimum requirement for plant growth in our study area (Bullied et al. 2006).

*Modeling individual variation in seasonal transition dates.*—In addition to modeling population-based seasonality, we calculated individual-specific seasonal transition dates using the same statistical procedure as described above, although without a random intercept for animal ID. To quantify individual differences in seasonal transition dates we subtracted the individual-specific date for the start of a particular season from the known population-level transition date. This provided us with a normally distributed (Shapiro test for normality:  $P > 0.25$  for all seasons) continuous variable with number of days as the unit. Positive values indicate delayed start of a season compared to the population level, whereas negative values indicate earlier start of a season compared to the population level.

To analyze differences in individual seasonal transition dates we used linear models with animal ID as the statistical unit. Covariates included sex, species, year, age class, elevation, predation risk by wolves, and their interactions. Age of GPS-collared white-tailed deer was estimated during field captures based on antler size, body mass, and tooth-wear patterns. All individuals were subsequently classified into 3 age classes ( $n = 1$  young,  $n = 7$  prime-age adults, and  $n = 1$  older adult). Age of

elk was determined by counting annuli in the cementum of incisor root tips (Hamlin et al. 2000). Because a continuous age variable for white-tailed deer was missing, we classified elk into the same 3 age classes as proposed by Wright et al. (2006):  $\leq 2$  years old ( $n = 3$  young), 3–9 years old ( $n = 12$  prime-age adults), and 10+ years ( $n = 3$  older adults). We used a digital elevation model (Supporting Information S1) to extract the mean elevation (m) for each individual separately at the date of the seasonal inflection point (i.e., the mean of 12 GPS locations at the day of a seasonal transition). We used distance to wolf as a proxy for predation risk (Liley and Creel 2008). Wolf locations were collected from very-high-frequency-collared animals between 2003 and 2006 from the air and ground ( $\bar{X} = 16$  wolves/week), which coincided with the period of the GPS-collared female elk and all of the white-tailed deer data. Distance to wolf (m) was calculated as the mean distance to the nearest known wolf using 12 GPS locations at the day of a seasonal transition. Although we only used locations of wolves for that specific day for most individual elk and white-tailed deer, we used wolf locations collected 1 day prior to the seasonal transition date for 2 female elk and 1 male white-tailed deer because wolf locations were absent at the actual seasonal transition day. Whenever distance to wolf was included in the final model, we excluded these 3 individuals to ensure the relation was still present, which was always the case. Distances to wolf locations were unknown for male elk because these data were collected during 2008 and 2010. Male elk data were therefore not considered when analyzing the effect of predation risk on individual variation in seasonal transition dates. Based on principles of parsimony, model selection was conducted by using the relatively conservative  $F$ -statistic and backward selection using  $\alpha = 0.05$  as the threshold for inclusion of predictor variables and their interactions (Murtaugh 2009). We validated the final models by checking homogeneity of the residuals versus the fitted values, and equal variances and independencies among within-group errors. We reported the amount of variation explained ( $R^2_{\text{adj}}$ ) for all final models.

## RESULTS

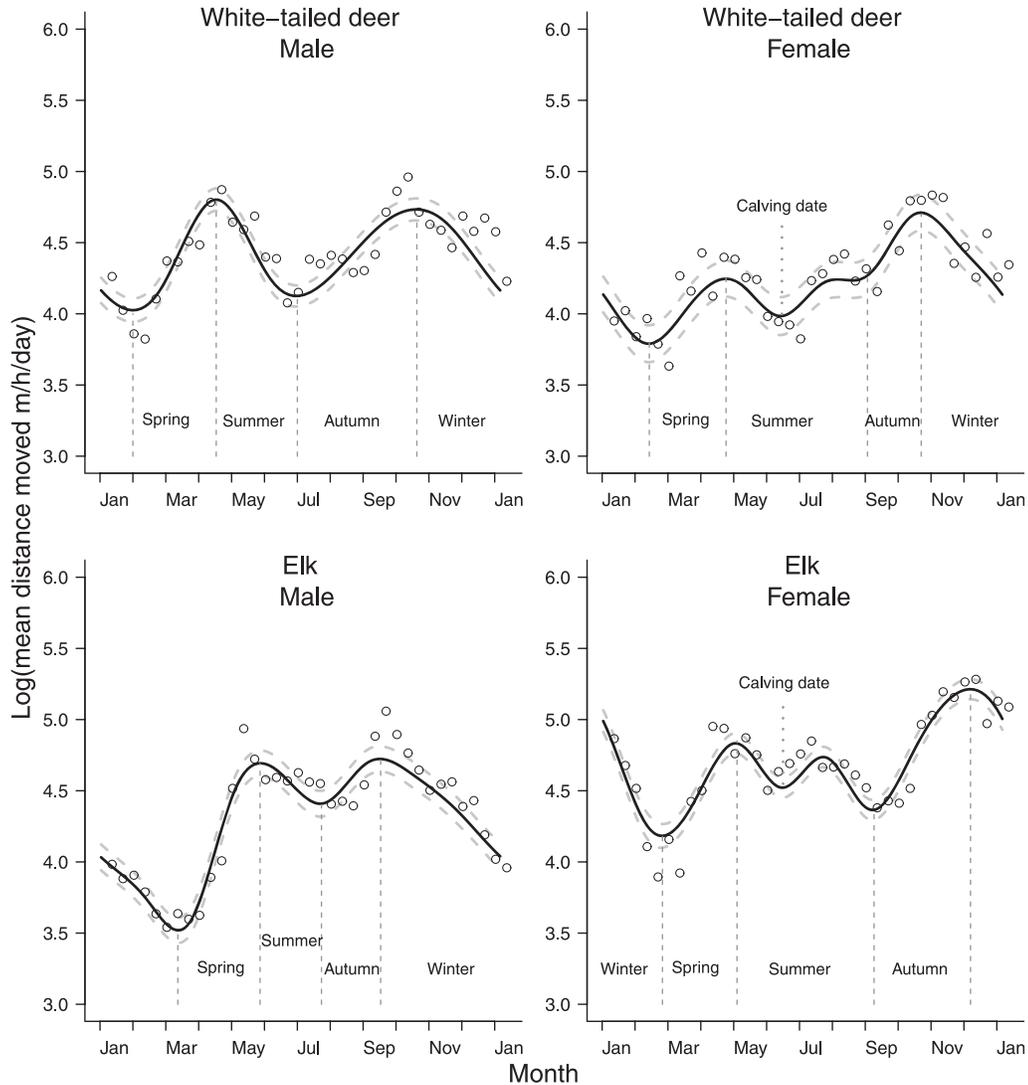
*Population-level seasonality.*—Movement rate varied nonlinearly over time (i.e., year) irrespective of species and sex (Fig. 1), which allowed for objective delineation of seasons (Table 1). With our approach, we identified 4 distinct seasons for male white-tailed deer and elk, and we were able to detect calving date for females as characterized by short-term (i.e., days) changes in movement rate in June. Predicted population-level mean calving date was similar between female elk (14 June) and white-tailed deer (13 June). Movement rate differed between species and sex ( $t$ -value = 6.3,  $P < 0.001$ ; Supporting Information S2, DOI: 10.1644/080.S2). Elk had higher movement rates than white-tailed deer (Tukey's honestly significant difference,  $P < 0.001$ ), male white-tailed deer had higher movement rates than female white-tailed deer (Tukey's honestly significant difference,  $P < 0.001$ ), whereas female elk

had higher movement rates than male elk (Tukey's honestly significant difference,  $P < 0.001$ ).

*Relating seasonal movement rate to environmental conditions.*—Species- and sex-specific movement rate during winter, as identified by our population-level model, was most strongly correlated (positive) with mean daily temperature (Supporting Information S3, DOI: 10.1644/080.S3; Pearson  $r = 0.34$ ,  $P = 0.002$  and  $r = 0.38$ ,  $P < 0.001$  for male and female white-tailed deer, respectively, and  $r = 0.4$ ,  $P < 0.001$  and  $r = 0.35$ ,  $P < 0.001$  for male and female elk, respectively). However, mean daily temperature during winter was negatively correlated with Julian day, which explained the decrease in movement rate during this season (Fig. 1). Similarly, movement rate of both species was most strongly correlated (negative) with mean daily temperature during summer (Pearson  $r = -0.36$ ,  $P < 0.001$  and  $r = -0.46$ ,  $P < 0.001$  for male and female white-tailed deer, respectively, and  $r = -0.35$ ,  $P < 0.001$  for male elk). Movement rate of female elk during summer was not significantly correlated to mean daily temperature (Pearson  $r = -0.09$ ,  $P = 0.564$ ) or GDD (Pearson  $r = -0.11$ ,  $P = 0.352$ ). Movement rate was positively correlated to GDD during spring (Pearson  $r = 0.44$ ,  $P < 0.001$  and  $r = 0.26$ ,  $P < 0.001$  for male and female white-tailed deer, respectively, and  $r = 0.29$ ,  $P < 0.001$  and  $r = 0.21$ ,  $P < 0.001$  for male and female elk, respectively). As expected, we did not detect any correlation between movement rate and ambient temperature or GDD during autumn (Supporting Information S3).

*Individual variation in seasonal transition dates.*—We observed considerable differences in timing and duration of seasonality when analyzing movement rate of each GPS-collared individual separately (Table 1). Start of winter was especially variable with a range of 126 days between the earliest (30 August for male elk) and latest (17 December for female elk) significant change in movement rate (i.e., inflection point).

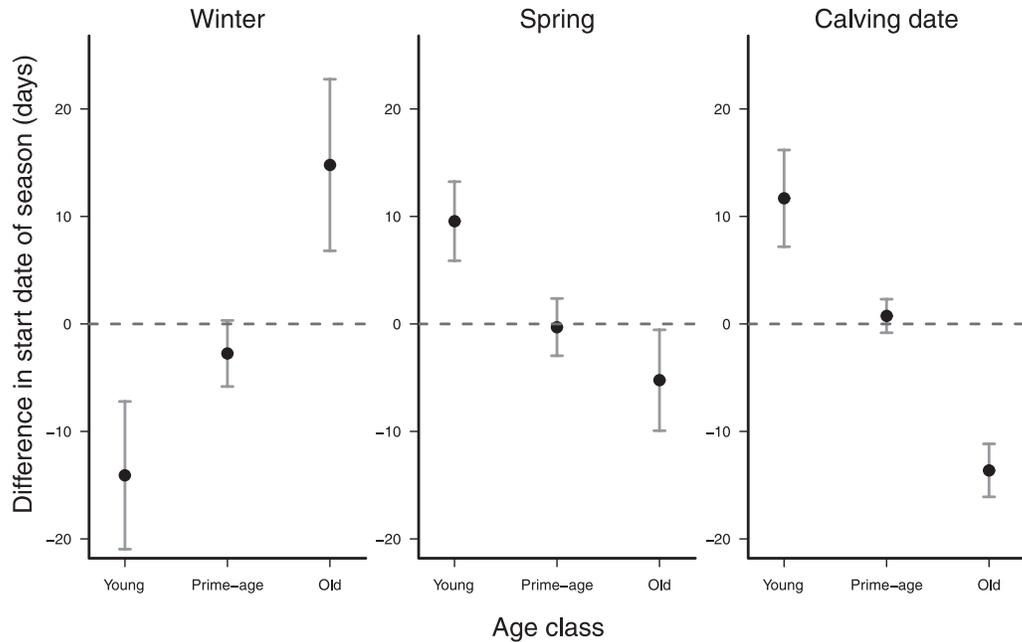
Irrespective of species and sex, age was an important factor in explaining variation in seasonal transition dates, at least during winter, spring, and calving date (Fig. 2; Table 2). Onset of winter was substantially earlier in young animals ( $\leq 2$  years old) compared to prime-age and older adults, whereas onset of spring and calving date were generally later for young animals compared to the other age classes. Model results also indicated that older females (10+ years) calved earlier compared to the other age classes. Elevation also explained considerable variation in seasonal transition dates (Fig. 3; Table 2), with individuals at lower elevations typically starting winter, spring, and calving season earlier than individuals at higher elevations. Wolf predation risk also influenced individual-based seasonal transition dates (Fig. 4; Table 2). Model results showed that individual elk and white-tailed deer that were close to wolves generally delayed start of spring, whereas the effect of distance to wolf on the onset of summer and autumn showed the reverse pattern. We did not find a significant effect of predation risk on calving date for either of the species. Between-year differences in seasonal transition dates were only observed for start of



**FIG. 1.**—Results of population-level generalized additive mixed model analysis showing predicted movement rate over a year for male and female elk and white-tailed deer. Seasons (winter, spring, summer, autumn, and calving date for females) are delineated based on inflection points (i.e., day with a significant change [increase or decrease] in movement rate). The plotted raw data points (open circles) are the population-level mean movement rates calculated over a 10-day period.

**TABLE 1.**—Summary of predicted population-level (mean) and individual-level (minimum [min], maximum [max]) seasonal transition dates for male ( $n = 6$ ) and female ( $n = 3$ ) white-tailed deer and for male ( $n = 7$ ) and female ( $n = 11$ ) elk in southwestern Manitoba, Canada. Dates were estimated by their inflection points (i.e., day with a significant change [increase or decrease] in movement rate).

	White-tailed deer		Elk	
	Male	Female	Male	Female
Population-level start winter	16 October	18 October	13 September	2 December
Individual-level min, max	18 September, 19 October	18 September, 2 November	30 August, 15 October	13 November, 17 December
Population-level start spring	30 January	12 February	12 March	24 February
Individual-level min, max	22 January, 7 March	8 February, 14 February	21 February, 18 March	19 February, 1 March
Population-level start summer	16 April	23 April	26 May	3 May
Individual-level min, max	2 April, 27 May	16 April, 28 April	19 May, 14 June	21 April, 6 June
Population-level calving date	—	13 June	—	14 June
Individual-level min, max	—	7 June, 16 June	—	1 June, 24 June
Population-level start autumn	29 June	30 August	21 July	5 September
Individual-level min, max	21 June, 29 July	18 August, 1 September	9 July, 8 August	14 August, 16 September



**FIG. 2.**—Plot showing the effect of age class on individual variation (elk and white-tailed deer combined) in seasonal transition date (days) for winter, spring, and calving date. Error bars represent 95% confidence interval. Positive values on the y-axis indicate delayed start of a season compared to the population level (horizontal line at 0), whereas negative values indicate earlier start of a season compared to the population level. Predictions were made while keeping other variables retained in the final models constant at their mean value.

spring (Table 2). We found no evidence of species or sex effects on individual differences in seasonal transition dates.

## DISCUSSION

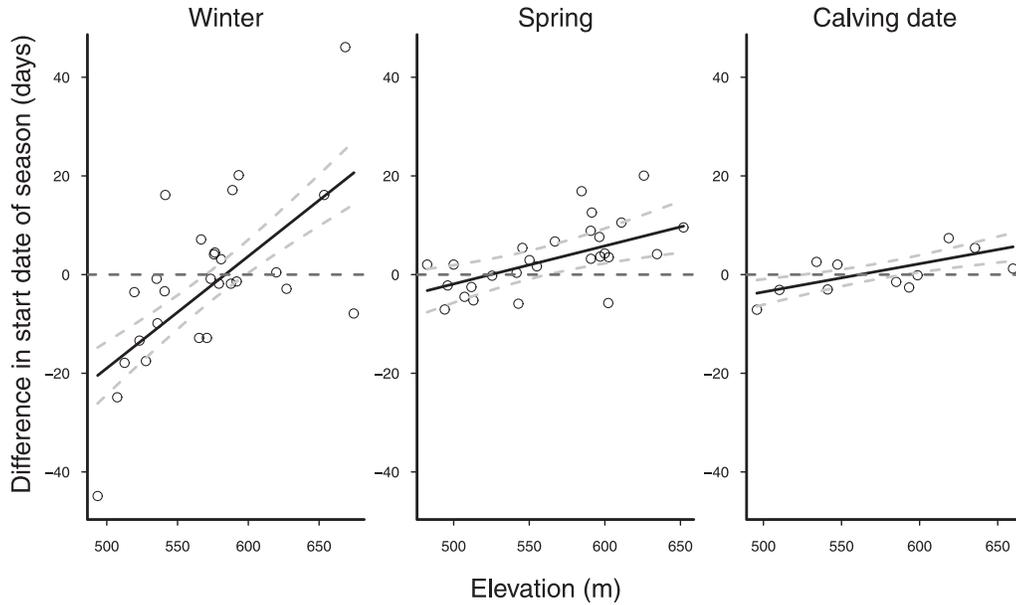
In this multispecies study we quantified temporal changes in movement rate, which facilitated objective delineation of 4 biologically meaningful seasons for both male and female elk and white-tailed deer. In addition, we showed how individual differences in seasonal transition dates were related to various intrinsic and extrinsic factors such as age class, predation risk by wolves, and elevation. Movement rate during winter, spring, and summer, as identified by our analytical framework, correlated strongly with mean ambient temperature (winter

and summer) or GDD (spring) as expected ( $P_{1a}$ – $P_{1c}$ ). Evidence of scale-dependent direct (e.g., ambient temperature) and indirect (e.g., GDD) effects of local climate on animal space-use patterns is increasing (Rivrud et al. 2010; van Beest et al. 2011). Our findings indicate that these environmental conditions also relate to seasonal-specific movement rates of elk and white-tailed deer.

In addition to identifying distinct ecological seasons, we were able to detect parturition date for both species using previously observed signatures in female movement rate ( $P_{1d}$ —Brook 2010; Dzialak et al. 2011). Moreover, model predictions of female elk calving date presented here ( $\bar{X}$  = 14 June; range = 1–24 June) are highly comparable to previous observational studies in the Riding Mountain National Park

**TABLE 2.**—Overview of the  $F$ -values and the direction of the relationship (+/–: + for positive relationships and – for negative relationships) of the fixed effects in the most-parsimonious models explaining variation in individual-level seasonal transition dates in winter, spring, summer, calving date, and autumn.  $R^2_{adj}$ -values show the amount of variation explained in each seasonal model. The models form the analytical basis for Figs. 2–4.

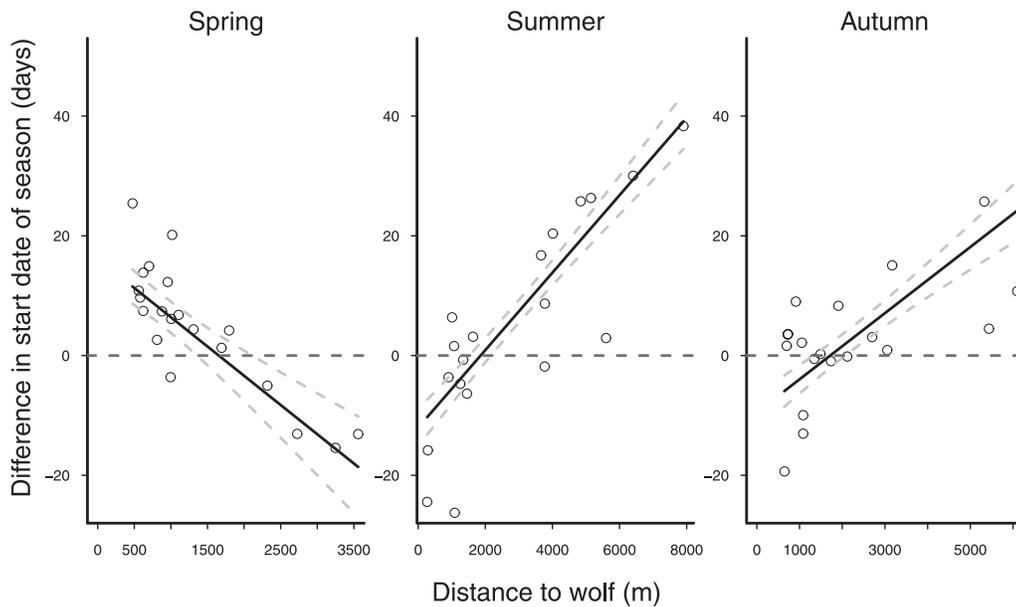
Season	Variable	+/–	<i>df.</i>	<i>F</i> -value	<i>P</i> -value	$R^2_{adj}$
Winter	Age class	+	2, 23	3.45	0.049	0.53
	Elevation (m)	+	1, 23	15.62	0.001	
Spring	Age class	–	2, 12	4.00	0.047	0.83
	Year	–	2, 12	11.48	0.002	
	Elevation (m)	+	1, 12	47.70	<0.001	
	Distance to wolf (m)	+	1, 12	14.10	0.003	
	Elevation × distance to wolf	–	1, 12	8.93	0.011	
Summer	Distance to wolf (m)	+	1, 17	59.03	<0.001	0.76
Calving date	Age class	–	2, 7	13.82	0.004	0.74
	Elevation (m)	+	1, 7	4.26	0.078	
Autumn	Distance to wolf (m)	+	1, 17	22.97	<0.001	0.55



**FIG. 3.**—Plot showing the effect of elevation (m) on individual variation (elk and white-tailed deer combined) in seasonal transition date (days) for winter, spring, and calving date. Note that the line for calving date shows a trend ( $P = 0.078$ ). Positive values on the y-axis indicate delayed start of a season compared to the population level (horizontal line at 0), whereas negative values indicate earlier start of a season compared to the population level. Lines show predicted values, and points are model residuals. Predictions were made while keeping other variables retained in the final models constant at their mean value.

area. For example, Paquet and Brook (2004) observed female elk with neonates between 25 May and 14 June, with a mean parturition date of 9 June. Movement rate during autumn was unrelated to any of the environmental conditions considered here but the observed stable increase in movement rate for both species and sexes is expected ( $P_{1c}$ ) during the rutting season

(Bowyer 1981; Webb et al. 2010). Similarities between expected biological responses and our model predictions suggest that our model captured the data adequately ( $R^2_{adj} = 0.76$ ; Supporting Information S2) and can be used effectively to define seasonality of nonmigratory large herbivores such as elk and white-tailed deer.



**FIG. 4.**—Plot showing the effect of distance to wolf (m) on individual variation (elk and white-tailed deer combined) in seasonal transition date (days) for spring, summer, and autumn. Positive values on the y-axis indicate delayed start of a season compared to the population level (horizontal line at 0), whereas negative values indicate earlier start of a season compared to the population level. Lines show predicted values, and points are model residuals. Predictions were made while keeping other variables retained in the final models constant at their mean value.

Movement rate differed between species, with higher annual movement rates for elk compared to white-tailed deer, which resulted in differences in timing and length of seasons (Fig. 1). Movement rates of male white-tailed deer were higher compared to females yet the reverse was observed for elk. Variation in body size and morphology (Harestad and Bunnell 1979; Underwood 1983) typically explains interspecific differences in movement rate rather well, whereas intraspecific (i.e., between sexes) differences in movement rate of large herbivores are less discrete because they are influenced by multiple variables including feeding strategy (Etzenhouser et al. 1998) and individual state or condition (Main et al. 1996). Male elk typically forage in areas with higher abundance of low-quality forage and have longer retention times of digesta in the rumen compared to females (Long et al. 2009). As a result male elk spent more time resting and ruminating, which likely explains the observed sexual differences in annual movement rate.

Variables such as forage abundance and quality (Festa-Bianchet 1988; Hebblewhite et al. 2008), predator avoidance (Festa-Bianchet 1988; Hebblewhite and Merrill 2009), and age (McCorquodale 2003; Wahlstrom and Liberg 1995) can influence migratory behavior (e.g., timing and duration of migration). Here we have shown that these variables also affect individual variation in seasonal transition in nonmigratory animals ( $P_2$ ), suggesting that similar extrinsic and intrinsic factors can influence both large- (i.e., migratory) and small-scale seasonal movement patterns. For example, age class was an important intrinsic variable because it explained much of the observed differences in individual timing of winter, spring, and calving date (Fig. 2). Start of winter was typically earlier for young individuals ( $\leq 2$  years) compared to older age classes, whereas the reverse relation was evident for start of spring and calving date. Such age-based differences in movement and seasonality may be related to previous experience and familiarity with the environment (Stamps 1995; Wolf et al. 2009). Moreover, factors influencing reproductive success in ungulates commonly differ between sexes and among age classes (Côté and Festa-Bianchet 2001; DelGiudice et al. 2007). The later date of parturition of young females compared to older females in this study is likely a signal of inexperience, especially considering that parental experience increases with age (Côté and Festa-Bianchet 2001; Ozoga and Verme 1986).

Wolves are known to influence movements of elk and white-tailed deer (Fortin et al. 2005; Nelson and Mech 1991) and proximity to wolves can initiate both short- and long-term range displacements in elk (Creel et al. 2005; Gower et al. 2009). Our results indicate that predation risk by wolves also affects timing of seasonal transition dates in nonmigratory populations such that individuals close to wolves change their season-dependent movement rate earlier than individuals inhabiting areas farther from wolves. We did not detect an effect of predation risk on calving date of either species, even though predation risk is considered an important selection pressure for birth synchronization (Ims 1990), which we did observe (mean calving date of elk of 14 June and white-tailed deer of 13 June). Rather, individual differences in calving date were positively related to

elevation, which agrees with recent suggestions that birth synchronization in large herbivores relates best to plant phenology rather than predation risk (Panzacchi et al. 2008; Post et al. 2003).

Elevation is often used as an environmental proxy for plant phenology and snow depth, which effectively describe timing of spring and autumn migration, respectively (Myserud 1999; Nelson 1995). Similarly, we found that for nonmigratory individuals the start of spring was positively related to elevation (Fig. 3), which is likely driven by spatial heterogeneity in forage quality across the altitudinal gradient in the study area. Individual differences in start of winter (i.e., end of autumn) also were positively affected by elevation (Fig. 3), a finding that contrasts with the expectation based on increased snow depth at higher elevations (Myserud 1999). A more likely explanation in this case is that individuals responded to localized hunting pressure outside Riding Mountain National Park because individuals at lower elevation often experience increased hunting risk due to the proximity to towns and roads (Conner et al. 2001; McCorquodale 2003), which may explain the earlier start of winter season at lower elevation in our study area.

The importance to define biological meaningful seasons in animal space-use studies is apparent and several analytical frameworks (of varying complexity) have recently been developed across a range of large herbivore populations (Basille et al. 2012; Birkett et al. 2012; Ferguson and Elkie 2004; Vander Wal and Rodgers 2009). Most of these studies are based on movement rate of individuals (but see Basille et al. 2012) because this behavioral parameter relates well to seasonal changes in environmental conditions, as shown here. Although it is possible to consider other parameters to delineate seasons objectively, such as path tortuosity, which is known to be influenced by foraging intensity and habitat selection (Nams 2005; Webb et al. 2009), a priori hypotheses about how alternative parameters change over time (i.e., seasons) need to be established and tested before being considered in studies of seasonality. Our approach is unique in that individual differences in onset of seasonality are easily determined. Such individual variation in movement rate and associated seasonal transition dates holds great potential to assess the effect of seasonality on space-use patterns, foraging behavior, differences in individual fitness, and ultimately population dynamics (Morales et al. 2010; Nicholson et al. 1997). For example, individual differences in date of parturition can affect calf survival (Keech et al. 1999; Singer et al. 1997) and development (Festa-Bianchet et al. 2000). Similar fitness effects may arise because of individual differences in the onset of spring, as the timing and duration at which animals can exploit high-quality forage has demographic implications across a variety of ungulates (Pettorelli et al. 2007; Post and Forchhammer 2008). Because identifying individual differences in onset of seasons or date of parturition of free-ranging herbivores often is difficult to observe in the field, our analytical

framework provides a useful tool to address such ecologically important questions.

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### SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Map of the study area showing the western side of Riding Mountain National Park (RMNP) in southwestern Manitoba, Canada, and the spatial distribution of global positioning system-collared elk ( $n = 18$ ) and white-tailed deer ( $n = 9$ ) and the digital elevation model (m).

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SUPPORTING INFORMATION S2.—Parameter estimates of the population-level generalized additive mixed model analysis predicting movement rates of global positioning system-collared elk and white-tailed deer in southern Manitoba, Canada. The model includes a random intercept for animal identification (ID) and a correlation structure (corRatio) for Julian day to account for temporal dependence in the data. The model forms the analytical basis for Fig. 1.

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SUPPORTING INFORMATION S3.—Plot showing correlations between seasonal movement rate and mean daily temperature (winter and summer) and growing degree days (spring) for each species and sex separately. Only significant correlations at  $\alpha = 0.05$  are depicted by a trend line.

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