

Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore

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Abstract Large herbivores are typically confronted by considerable spatial and temporal variation in forage abundance and predation risk. Although animals can employ a range of behaviours to balance these limiting factors, scale-dependent movement patterns are expected to be an effective strategy to reduce predation risk and optimise foraging opportunities. We tested this prediction by quantifying site fidelity of global positioning system-collared, non-migratory female elk (*Cervus canadensis manitobensis*) across multiple nested temporal scales using a long-established elk–wolf (*Canis lupus*) system in Manitoba, Canada. Using a hierarchical analytical approach, we determined the combined effect of forage abundance and predation risk on variation in site fidelity within four

seasons across four nested temporal scales: monthly, biweekly, weekly, daily. Site fidelity of female elk was positively related to forage-rich habitat across all seasons and most temporal scales. At the biweekly, weekly and daily scales, elk became increasingly attached to low forage habitat when risk was high (e.g. when wolves were close or pack sizes were large), which supports the notion that predator-avoidance movements lead to a trade-off between energetic requirements and safety. Unexpectedly, predation risk at the monthly scale increased fidelity, which may indicate that elk use multiple behavioural responses (e.g. movement, vigilance, and aggregation) simultaneously to dilute predation risk, especially at longer temporal scales. Our study clearly shows that forage abundance and predation risk are important scale-dependent determinants of variation in site fidelity of non-migratory female elk and that their combined effect is most apparent at short temporal scales. Insight into the scale-dependent behavioural responses of ungulate populations to limiting factors such as predation risk and forage variability is essential to infer the fitness costs incurred.

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Introduction

Understanding why animals return to a previously occupied area or remain within the same area for extended time (i.e. site fidelity) are major questions in ecology because of the implications for individual fitness and population dynamics (White and Garrott 1990; Switzer 1993; Ortega et al. 2006; Piper 2011). Fidelity to a particular space can enhance survival and reproductive success, which has been shown

across a range of taxa (see Switzer 1993; Oliver et al. 1998 for detailed reviews), and is commonly attributed to familiarity with the distribution of: (1) forage resources, (2) conspecifics, and (3) predators (Schaefer et al. 2000; Kirk et al. 2008; Wolf et al. 2009). As such, quantifying site fidelity may be an effective approach to determine how individuals balance demands for food and safety. Fidelity varies across multiple spatial and temporal scales for diverse taxa, including fine-scaled sleeping sites (Clark and Gillingham 1990), and foraging sites (Kirk et al. 2008) as well as relatively coarse-scale breeding areas (Schieck and Hannon 1989), foraging areas (Broderick et al. 2007), and territories (Young and Franklin 2004).

For ungulates, site fidelity has been predominantly quantified at coarse spatial scales using annual or seasonal home ranges (Edge et al. 1985; Wittmer et al. 2006; Wiseman et al. 2006). Indeed, fidelity to distinct annual or seasonal ranges via e.g. long-distance migration is commonly considered one of the most effective behavioural strategies of ungulates to reduce predation risk and optimize foraging opportunities (Bergerud 1988; Fryxell et al. 1988). Non-migratory species, or populations incapable of migrating seasonally due to habitat loss or landscape fragmentation (Berger 2004), must employ alternative movement strategies at fine spatiotemporal scales to balance these limiting factors (Rettie and Messier 2001). However, few studies have examined the concurrent effect of forage abundance and predation risk on intra-specific variation in site fidelity of non-migratory populations (but see Gower et al. 2009) and the potential for scale-dependence is rarely considered in detail (Schaefer et al. 2000; Faille et al. 2010).

At coarse spatial and temporal scales theoretical models predict that prey movement should be aimed at remaining unpredictable in space to reduce the likelihood of detection and encounters with predators (Mitchell and Lima 2002), often at the expense of energy intake (Lima and Dill 1990; Christianson and Creel 2010). However, when prey are familiar with site-specific habitat and mortality risks (e.g. experience gained through site fidelity; Wolf et al. 2009), the optimal space use strategy to maximize individual survival remains movement-directed towards richer food patches (Mitchell and Lima 2002). Indeed, elk unfamiliar with predation risk that were translocated into a novel system with multiple predators showed relatively high movement rates, low annual site fidelity, and reduced survival likely due to increased encounters with predators (Frair et al. 2007). At short temporal scales, elk in Yellowstone National Park (YNP) temporarily leave forage-rich patches when wolves are present, or following a predation event to avoid further threat, but typically return to previously occupied forage sites after several days or even hours (Creel et al. 2005; Gower et al. 2009). These

results suggest that site fidelity of elk should be positively related to forage-rich areas but that predation risk will cause changes in the direction of movement and habitat occupancy leading to an overall reduction in site fidelity, especially at short temporal scales.

The main objective of this study is to examine the concurrent effect of forage abundance and predation risk by wolves (*Canis lupus*) on variation in site fidelity of non-migratory female prairie-parkland elk (*Cervus canadensis manitobensis*) in a long-established predator-prey system (Riding Mountain National Park; RMNP) in southern Manitoba, Canada. We considered several, relatively fine temporal scales within seasons (i.e. monthly, biweekly, weekly, and daily) to test for scale-dependent effects of these factors on intra-specific site fidelity. These temporal scales reflect a gradient of behavioural processes (e.g. month = relatively fine-scaled habitat selection and day = foraging), in which spatial familiarity, the main driver of site fidelity (Schaefer et al. 2000), is expected to play a crucial role (Wolf et al. 2009). We test the following two predictions:

Prediction 1

We expect within-season site fidelity of adult female elk familiar with predation risk by wolves to be positively related to forage abundance, a pattern that should be evident across all temporal scales (P.1).

Prediction 2

We expect the effect of predation risk on within-season site fidelity of non-migratory female elk in our study area to be scale-dependent. If elk in RMNP respond to predators on short temporal scales with fine-scale, dynamic predator-avoidance movements when predation risk is high but return to previous sites once predation risk is low or absent (as in YNP), we expect site fidelity at long temporal scales to be unrelated to predation risk (>week; P.2.1) but negatively related to predation risk at short temporal scales (≤week; P.2.2).

Materials and methods

Study area

The study area is located in the Prairie and Boreal Plain ecozones in south-western Manitoba, Canada. The area includes RMNP, a relatively undisturbed, forested area of 2,974 km² (50°51'N, 100°15'W). Most of the area outside of RMNP is under intensive agriculture with large fields of annual cereal and oilseed crop and perennial forage cropland, as well as pasture for beef cattle (Brook 2010). The

elk population is spatially restricted to RMNP and its immediate surroundings (within 10 km) and as such is non-migratory (Brook 2010; Vander Wal et al. 2012). Winter densities of elk in RMNP were estimated at approximately 0.86 and 0.77 elk per km² in 2003 and 2004, respectively (Vander Wal et al. 2013). Winter surveys also indicated a relatively stable wolf population (approximately 75 individuals) present in the area since 1976. Elk are the dominant food item for wolves in this area, both in frequency of occurrence and biomass consumed, while black bears and cougars only rarely consume adult elk in RMNP (Paquet 1992).

Elk data

Adult (>3 years old; based on body size, and cementum aging) female elk ($n = 25$) were captured between December 2003 and March 2004 using a net gun fired from a helicopter. Each individual was fitted with a global positioning system (GPS) satellite collar programmed with a 2-h relocation schedule for up to 1 year. Spatial error associated with the GPS collars (mean \pm SE = 14 \pm 2 m) was determined by placing collars at known locations for several hours. All GPS locations collected within 24 h of capture were excluded, which is typically done when assessing fine-scale animal space-use patterns (Rivrud et al. 2010; van Beest et al. 2011). We screened the GPS data for positional outliers using an established technique (Bjørneraas et al. 2010). This approach identifies erroneous fixes based on impossible speed of movement (in our case this was set at 30 km/h as we thought it unlikely female elk would move at this speed between two location attempts) in combination with turning angles >166° but <194° (i.e. the animal is returning in roughly the same direction it came from). With this approach we removed 213 outliers (<0.1 % of the full GPS data set). Collar failure reduced the number of full-year GPS datasets to 21 individuals. However, not all individuals were used in each seasonal/temporal scale analysis (see Table 1 for final sample size across temporal scales) because of insufficient coverage (e.g. we selected only adult females with at least 95 % coverage for a given time interval in order to calculate robust and comparative home ranges) or unknown predation risk information at the daily scale (see section on Wolf data and predation risk covariates below). None of the GPS-collared individuals included in our analyses were predated by wolves during the study period.

Quantifying home range size and site fidelity across temporal scales

Site fidelity is typically quantified by the degree of spatial overlap between consecutive home ranges (Doncaster and

Table 1 Overview of the model structure used to analyse variation in site fidelity of female elk across temporal scales

Timescale and model structure	Winter	Spring	Summer	Autumn
Month				
Statistical analysis	LME	LME	GLS	GLS
Elk ID	1.159	0.824	NA	NA
Spatial correlation	NA	NA	1,802 <i>m</i>	NA
Variance	NA	NA	-0.807	-0.35
<i>n</i>	14	17	15	14
Biweekly				
Statistical analysis	GLS	LME	GLS	LME
Elk ID	NA	0.264	NA	0.201
Spatial correlation	NA	445 <i>m</i>	562 <i>m</i>	NA
Variance	-0.198	NA	-0.332	-0.216
<i>n</i>	15	18	17	14
Week				
Statistical analysis	LME	LME	GLS	GLS
Elk ID	0.119	0.212	NA	NA
Spatial correlation	NA	NA	223 <i>m</i>	340 <i>m</i>
Variance	-0.680	-0.374	-0.199	-0.135
<i>n</i>	17	17	17	14
Day				
Statistical analysis	LME	LME	LME	GLS
Elk ID	0.334	0.319	0.562	NA
Spatial correlation	106 <i>m</i>	241 <i>m</i>	NA	211 <i>m</i>
Variance function	-0.345	-0.511	-0.63	-0.373
<i>n</i>	17	18	15	15

Statistical analysis shows the model function used as implemented in the statistical package R. Elk identity (*ID*) shows the SD of the random intercept in the full mixed-effects model. Spatial correlation indicates the range of the spatial autocorrelation (*m*), and variance indicates the amount of heterogeneity in model residuals, corrected for in the models

LME Linear mixed models, *GLS* generalized least squares, *n* the number of individuals included in the analyses, *NA* not used in the analyses

Macdonald 1991; Kernohan et al. 2001) although other techniques can be used (Gower et al. 2009). We estimated home ranges and spatial overlap for each individual separately across four temporal scales within each season [i.e. monthly, biweekly (2 weeks), weekly, and daily]. These temporal scales have previously been identified as appropriate time scales to investigate direct and indirect effects of environmental conditions (including forage abundance) on animal space use (Rivrud et al. 2010; van Beest et al. 2011). Moreover, spatial familiarity with forage abundance and predation risk is expected to influence scale-dependent movements of animals at such fine temporal scales (Wolf et al. 2009; Prediction 2). Because GPS collar data from individual elk were collected over the course of 1 year

only, we were unable to estimate home range overlap at the seasonal scale due to lack of repeated observations across years. All temporal scales were analysed separately within four distinct seasons that were delineated based on changes in female elk movement rate during the year (van Beest et al. 2013). As such, we defined winter as the period between 30 November and 15 March, spring from 16 March to 31 May, summer from 1 June to 12 August and autumn from 13 August to November. Home ranges and overlap were subsequently estimated using the fixed kernel utilization distributions (95 % UDs) and the volume of intersection (VI) as recommended by previous studies (Millspaugh et al. 2004; Fieberg and Kochanny 2005). All UDs were estimated using the reference technique for the calculation of the smoothing factor h (Kernohan et al. 2001). UDs and VI were estimated using the library `adehabitat` implemented in R (R Development Core Team 2012).

Forage abundance

We considered eight vegetation communities known to affect elk space use (Fortin et al. 2005; Hebblewhite and Merrill 2008; Brook 2010) and that differ strongly in forage abundance: coniferous, deciduous, and mixed conifer/deciduous forests, grasslands, wetlands (primarily marsh), annual cropland, pastures (and perennial cropland), and water (including lakes, streams, and rivers). We ranked the vegetation types according to seasonal variation in forage abundance using field-based vegetation cover collected in 202 sample plots (100 m²) located in different vegetation types throughout the study area (see Table A1, Online Resource 1, for a detailed description of seasonal ranking based on forage abundance). For each consecutive home range overlap area we calculated the proportion of each vegetation type present using the open-source Geospatial Modelling Environment (www.spatialecology.com).

Wolf data and predation risk covariates

Wolves (six males and 12 females within eight different packs) were captured during the winters of 2003 and 2004 using a net gun fired from a helicopter. All wolves were fitted with a VHF collar. Wolves were located from the air and ground (mean = 16 locations per week) during 2003–2006, which coincided with the period of the GPS-collared elk data. During each visual observation, we recorded the location of the VHF-collared wolf along with the number of wolves present in the pack (mean pack size 5, range 1–16 wolves).

Predation risk is often quantified as a dichotomous temporal variable (e.g. safe vs. dangerous periods); however, a more useful approach may be to quantify risk as a

spatial continuum or a risk gradient (Liley and Creel 2008). We used the following indices of predation risk to determine the effect on site fidelity of elk: (1) minimum distance to wolf, (2) mean distance to wolf, (3) maximum distance to wolf, and (4) pack size of nearest wolf. To calculate these, locations of wolves were used to create landscape-level raster layers (50 m × 50 m pixel size) in ArcGIS 10 (2010 ESRI, Redlands, CA). In our case, each pixel in a raster represented either the distance (metres) to the nearest wolf on the landscape or the pack size of the nearest wolf. We then used the function `zonal statistics` in ArcGIS 10 to extract statistics (e.g. the minimum, mean, and maximum) on the values of a raster (e.g. distance to nearest wolf) for within each consecutive overlapping home range of an individual elk (i.e. where site fidelity occurs). Thus, the minimum and maximum distance to wolf were the lowest and highest pixel value found within each overlapping home range area, while the mean distance to nearest wolf was calculated by averaging all pixels values within the total overlapping home range area.

Wolf observations were less frequent and less accurate spatially than locations obtained for elk, and separate raster layers were created for each temporal scale using only positions of wolves that were visually observed during a particular time period. The inconsistency between wolf and elk sampling intensity forced us to reduce the elk dataset to those days where wolf observations were successful and as such predation risk measurements known. Despite these limitations, sample sizes (Table 1) were considered sufficient to test for variation in site fidelity across the temporal scales considered here.

Model development and statistical analyses

To examine variation in site fidelity of adult female elk as a function of forage abundance and predation risk across multiple temporal scales, we used an analytical procedure appropriate for repeated measurement (Börger et al. 2006; van Beest et al. 2011). We fitted linear mixed models (LME) from the R library `nlme` (Pinheiro and Bates 2000). Proportion of home range overlap was logit-transformed (Warton and Hui 2011) and fitted as the response variable in all models. Habitat type (a proxy for forage abundance), measures of predation risk and their interaction were fitted as fixed effects in the global models. We did not consider three-way interactions here due to sample size constraints, especially at longer temporal scales. We screened for correlations and collinearity among fixed effects using Pearson's correlation and variance inflation factors (VIF). When two covariates were correlated (Pearson $r > 0.5$ or VIF > 3) we removed one of the covariates. For example, due to multicollinearity between predation risk indices: minimum, mean, and maximum distance to wolf, we only

Table 2 Model-averaged effects of habitat type, with varying forage abundance, and predation risk indices on site fidelity of female elk across temporal scales

Timescale and fixed effects	Winter			Spring			Summer			Autumn		
	β	SE	$w_+(\hat{t})$	β	SE	$w_+(\hat{t})$	β	SE	$w_+(\hat{t})$	β	SE	$w_+(\hat{t})$
	Monthly											
Prop. coniferous forest	-12.65	3.13	0.74*	-	-	-	-	-	-	-90.97	8.62	1*
Prop. mixed forest	15.07	3.39	0.74*	-	-	-	-	-	-	19.09	2.85	1*
Prop. deciduous forest	-	-	-	-	-	-	-	-	-	1.27	0.34	0.88*
Prop. annual cropland	-	-	-	2.98	0.39	1*	3.59	1.41	1*	-	-	-
Prop. pasture and perennial cropland	-	-	-	6.64	5.66	0.22	-	-	-	-	-	-
Prop. grassland	8.30	2.01	1*	-	-	-	-	-	-	-	-	-
Prop. wetland	-	-	-	-1.36	1.16	0.22	-	-	-	-	-	-
Min. distance to wolf (m)	-0.0003	0.0001	0.26*	-0.0006	0.0001	1*	-0.0004	0.0002	1*	-	-	-
Pack size closest wolf	-	-	-	-	-	-	0.10	0.06	0.66	-	-	-
Biweekly												
Prop. coniferous forest	-	-	-	55.89	26.33	0.91*	-	-	-	-	-	-
Prop. mixed forest	10.95	3.23	1*	-	-	-	-	-	-	-	-	-
Prop. deciduous forest	-	-	-	-	-	-	-	-	-	1.88	0.64	1*
Prop. annual cropland	-0.25	0.12	0.66	1.09	0.86	0.12	3.77	1.60	1*	-	-	-
Prop. wetland	-	-	-	-17.66	14.44	0.45	-9.47	7.37	0.73	4.52	1.94	1*
Prop. water	7.19	3.15	0.77*	-	-	-	-	-	-	-	-	-
Min. distance to wolf (m)	-	-	-	-0.0001	0.0001	0.12	-0.0003	0.0001	1*	-0.001	0.0003	1*
Pack size closest wolf	-	-	-	0.05	0.24	0.8	0.17	0.09	0.73	-	-	-
Prop. wetland \times pack size	-	-	-	2.34	1.11	0.34*	1.29	0.88	0.73*	-	-	-
Prop. wetland \times distance to wolf	-	-	-	-	-	-	-	-	-	0.001	0.001	0.38
Weekly												
Prop. coniferous forest	-	-	-	-	-	-	-	-	-	0.50	8.49	1
Prop. mixed forest	0.53	2.21	1	-	-	-	-	-	-	-	-	-
Prop. deciduous forest	-	-	-	-	-	-	-	-	-	3.75	2.06	1
Prop. annual cropland	-	-	-	3.83	0.47	1*	3.32	0.65	1*	-	-	-
Prop. pasture and perennial cropland	-	-	-	-30.94	12.91	1*	-	-	-	-	-	-
Prop. grassland	-7.74	1.29	1*	-	-	-	-	-	-	-	-	-
Prop. wetland	-	-	-	-	-	-	-1.97	1.30	0.28	-	-	-
Prop. water	2.98	0.39	0.22	14.28	7.60	1*	-	-	-	-	-	-
Min. distance to wolf (m)	0.0002	0.0001	1	-0.0002	0.0001	1	-0.0003	0.0001	1*	-0.0001	0.0001	1*
Pack size closest wolf	-0.11	0.05	0.35*	-0.06	0.08	0.77	-	-	-	-0.01	0.17	1

Table 2 continued

Timescale and fixed effects	Winter			Spring			Summer			Autumn		
	β	SE	$w_{+}(j)$	β	SE	$w_{+}(j)$	β	SE	$w_{+}(j)$	β	SE	$w_{+}(j)$
	Prop. water X distance to wolf	-0.01	0.002	1*	-	-	-	-	-	-	-	-
Prop. pasture \times pack size	-	-	-	-2.08	0.90	0.77*	-	-	-	-	-	-
Prop. wetlands \times distance to wolf	-	-	-	-	-	-	0.002	0.0008	0.28*	-	-	-
Prop. coniferous \times distance to wolf	-	-	-	-	-	-	-	-	-	-0.01	0.004	1*
Prop. deciduous \times pack size	-	-	-	-	-	-	-	-	-	-0.33	0.23	0.61
Daily												
Prop. mixed forest	-2.34	0.79	1*	-	-	-	1.07	0.47	1*	-	-	-
Prop. deciduous forest	1.28	0.27	1*	-	-	-	-0.66	0.28	1*	1.91	0.29	1*
Prop. annual cropland	-	-	-	1.76	0.86	1*	0.34	0.33	0.21	-	-	-
Prop. grassland	-	-	-	-	-	-	1.58	0.41	1*	6.54	2.35	1*
Prop. wetland	-	-	-	-9.04	3.47	1*	0.98	0.60	0.21	-3.97	2.53	1
Prop. water	4.09	0.78	1*	-	-	-	-	-	-	-	-	-
Min. distance to wolf (m)	0.0001	0.0001	1*	-0.0001	0.0001	1	0.0001	0.0001	1	0.0002	0.0003	1*
Pack size closest wolf	-0.03	0.04	0.26	-	-	-	-	-	-	0.24	0.06	1*
Prop. mixed \times distance to wolf	-0.0001	0.0001	0.18	-	-	-	-	-	-	-	-	-
Prop. wetland \times distance to wolf	-	-	-	-0.001	0.0004	0.45*	-	-	-	-	-	-
Prop. wetland \times pack size	-	-	-	-	-	-	-	-	-	0.36	0.36	0.31
Prop. cropland \times distance to wolf	-	-	-	-	-	-	-0.0002	0.0001	0.21*	-	-	-
Prop. grassland \times distance to wolf	-	-	-	-	-	-	-0.0001	0.0001	0.5	-	-	-
Prop. deciduous \times distance to wolf	-	-	-	-	-	-	-	-	-	0.001	0.0002	1*

Regression coefficients (β) and adjusted SE as well as relative variable importance [$w_{+}(j)$] are provided for all covariates retained in the top ranked models. *Missing values* indicate that the variable was not included in the top ranked model for a particular temporal scale

Prop. Proportion, *Min.* minimum

* $P = 0.05$ [$w_{+}(j)$ of covariates indicate a significant difference from 0]

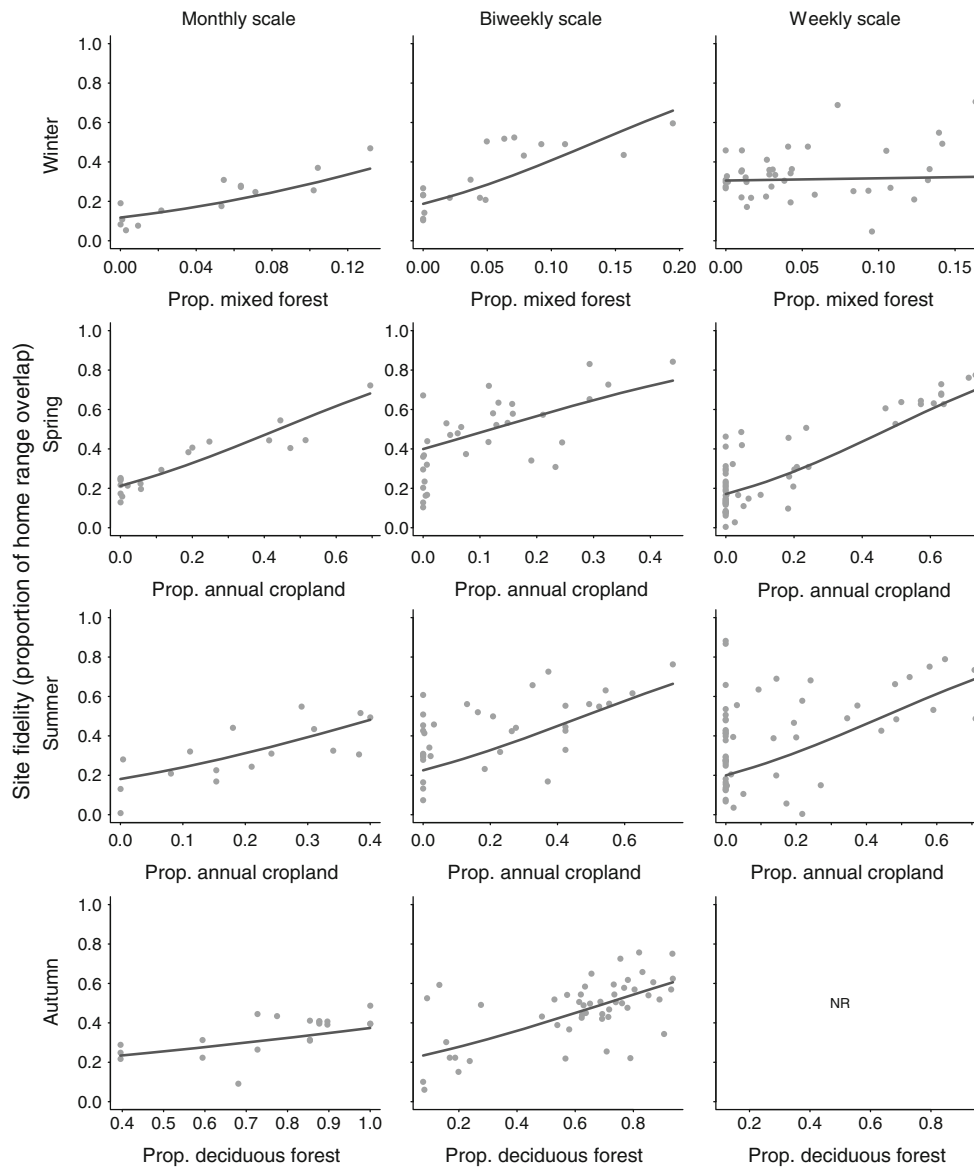


Fig. 1 Main effect of forage-abundant habitat types on site fidelity of female elk in southern Manitoba, Canada. *Panels* show the mean predicted level of increase in site fidelity [proportion (*Prop.*) of home range overlap] for each season and monthly, biweekly and weekly temporal scales. Predictions were made while keeping other variables

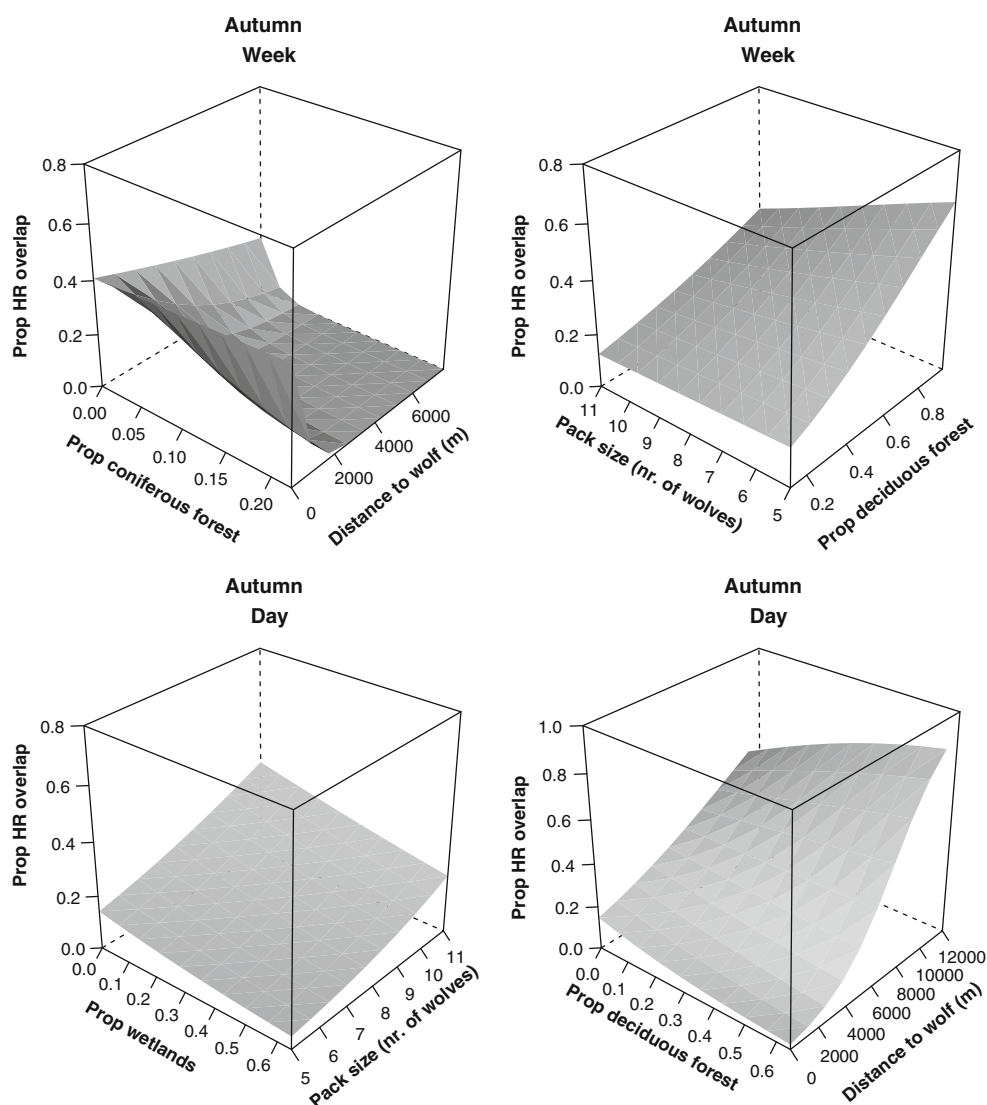
in the models constant at their mean value. *Lines* show predicted values (back-transformed using anti-logit), and *points* are model residuals. The main effect of proportion of deciduous forest on weekly site fidelity during autumn is not plotted in this figure as the relation was dependent on predation-risk levels (see Fig. 2)

included the minimum and maximum distance to wolves in subsequent analyses as we expected the effect on site fidelity to be most pronounced at the extremes of the risk gradient.

Elk identity (ID) was fitted as a random intercept to account for potential patterns in the residuals (Pinheiro and Bates 2000). We used likelihood ratio tests to evaluate if the mixed-effects model provided a better fit than a linear model without a random term. If the mixed-effects model was not significantly better than a linear model, we continued with generalized least squares (GLS) models. To estimate any residual dependence among observations we

considered either spatial or temporal correlation structures. Spatial correlation in site fidelity was modelled using the harmonic mean of the overlapping area between two consecutive home ranges. Temporal (serial) correlation structures are used to model dependence in time-series data where the event of interest occurs sequentially over time (Pinheiro and Bates 2000). In our case, temporal correlation was modelled by numbering the occasion's site fidelity which occurred within a given temporal scale for each individual separately. In all cases where a correlation structure improved model fit, we used the corExp function to model spatial correlation as this method provided the

Fig. 2 Interactive effect between forage abundance and predation risk on weekly and daily site fidelity during autumn for female elk in southern Manitoba, Canada. *Panels on the left* show how site fidelity to low forage-abundant habitat increased when predation risk increased, while *panels on the right* show how site fidelity for high forage-abundant habitat decreased when predation risk increased. Predictions were made while keeping other variables in the models constant at their mean value



best fit based on Akaike's information criterion (AIC) and visual inspection of diagnostic plots. Modelling temporal correlation never provided a better model fit for our data, so we only considered spatial correlation functions. We also checked for homogeneity of variance of model residuals, and incorporated variance functions if heterogeneity was observed. In all cases where a variance function improved model fit (based on AIC and diagnostic plots), we used the fitted values as the variance covariate using the varPower function.

When the distributional assumptions of the global model structure were fulfilled (Table 1), model selection was conducted using a multi-model inference technique based on model averaging (Burnham and Anderson 2002). As we limited inference to a minimum number of non-correlated variables known to affect elk space use, our set of candidate models consisted of all possible combinations of non-correlated independent variables (Burnham and Anderson

2002). We considered models with ΔAIC_{ci} (i.e. the difference between the top ranked model and other candidate models) < 2 to have substantial empirical support and calculated model-averaged coefficients and unconditional SEs for covariates using the R library MuMIn. Models were fitted using the maximum-likelihood estimation, which is necessary when comparing mixed-effects models or models with correlation structures with different fixed effects (Pinheiro and Bates 2000). We also calculated the relative variable importance [$w_+(j)$] for each covariate by summing the Akaike's weights (w) across all the models in the set where variable j occurred. The larger the $w_+(j)$ the more important variable j is (Burnham and Anderson 2002). To assess the amount of variation explained by the top ranked models ($\Delta AIC_{ci} < 2$), we used a generalized R^2 suitable for both LME and GLS, which is calculated as the square of the correlation between the fitted values of the model and the observed values in the data (Zheng and Agresti 2000).

Results

We observed considerable intra-specific variation in home range size and site fidelity of female elk across seasons and within nested temporal scales (Fig. A1, Online Resource 2). Forage abundance and predation risk were important determinants of female elk site fidelity across all temporal scales (Table 2) as the top ranked models (Tables A2–A5, Online Resource 3) explained between 63 and 85 % of the observed variation in proportion of home range overlap, being greater for monthly scales (mean = 82 %, range = 79–85 %) than daily scales (mean = 71 %, range = 63–76 %). Although the relation between covariates and site fidelity varied in strength [in terms of SE and $w_+(j)$] among the top models considered for model averaging, we did not detect quantitative changes in the direction of relationships (switch from positive β coefficients to negative or vice versa) at any of the temporal scales.

As expected (P.1), site fidelity was positively related to the proportion of forage-rich habitat present within overlapping home ranges across all seasons and most temporal scales (\geq week) independent of predation risk (Fig. 1; Table 2). One exception was found during autumn at the weekly scale as site fidelity to forage-rich deciduous forest varied depending on pack size of the closest wolf ($\beta_{\text{prop deciduous forest} \times \text{pack size}} = -0.33$; Fig. 2; Table 2).

Contrary to P.2.1, we found that predation risk was an important determinant of female elk site fidelity at the longest temporal scales (monthly and biweekly). Site fidelity at the monthly scale was negatively related to distance to wolf (i.e. increased site fidelity when predation risk was high) in most seasons [$\beta_{\text{distance to wolf (m)}} = -3.02 \times 10^{-4}$, -6.28×10^{-4} , -4.03×10^{-4} for winter, spring, and summer, respectively; Table 2]. During autumn, predation risk was not included in our final model (i.e. no effect on monthly site fidelity), which was also the case for biweekly site fidelity during winter (conform P.2.1). In other seasons predation risk influenced biweekly site fidelity through an interaction with low forage-abundance wetlands (Fig. A2, Online Resource 4), which showed increased site fidelity to wetlands when pack size of the closest wolf increased (spring and summer) as well as when distance to wolf decreased (autumn).

At the finest temporal scales (weekly and daily), site fidelity was clearly influenced by an interactive effect between forage abundance and predation risk (Table 2). In general, site fidelity decreased with increasing predation risk (as expected by P. 2.2) but this relation was evident for high forage-abundance habitat only. In contrast, when predation risk was high, female elk increased site fidelity to low forage-abundance habitat, a pattern that was recurrent across seasons. For example, during autumn we found that

weekly fidelity to coniferous forest (low forage habitat) increased only when wolves were close (i.e. predation risk was high), while at the same time fidelity to deciduous forest (high forage habitat) was highest when pack size of the closest wolf was small (five individuals) and decreased with increasing pack size (Fig. 2). A similar pattern was found at the daily scale as site fidelity to forage-rich habitat (deciduous forest) increased with increasing distance to the closest wolf (negatively related to predation risk) while fidelity to forage-poor habitat (wetlands) increased with increasing pack size (positively related to predation risk; Fig. 2). Comparable interactive effects between forage abundance and predation risk on weekly and daily site fidelity were also apparent during winter, spring, and summer (Figs. A3–A5, Online Resource 4). These relations included increased site fidelity to high forage-abundant habitat as predation risk decreased (daily scale winter, weekly scale spring, and daily scale summer), or increased site fidelity to low forage-abundant habitat as predation risk increased (weekly scale winter, daily scale spring, and weekly scale summer).

Discussion

Most ungulates are frequently confronted with spatiotemporal fluctuations in the availability of forage resources and predation risk (Fryxell et al. 1988; Tveraa et al. 2003; Kittle et al. 2008), which represents an important trade-off in animal behaviour. Here, we provide a comprehensive empirical evaluation of the concurrent effect of both of these limiting factors on the movement behaviour of non-migratory female elk across multiple nested temporal scales and seasons. Our study shows that the relative effect of habitat types with divergent forage abundance and predation risk by wolves on female elk site fidelity differed across temporal scales. Furthermore, we demonstrate that these bottom-up and top-down processes often interact within temporal scales, supporting the contention that the mechanisms of site fidelity are scale-dependent (Schaefer et al. 2000; Faille et al. 2010).

Given the importance of forage resources in the distribution of herbivore populations (Wittmer et al. 2006; Wolf et al. 2009; van Beest et al. 2011) it is not surprising that site fidelity of female elk was positively related to forage-abundant habitat in all seasons and most temporal scales (Fig. 1; supporting Prediction 1). Although this relation was independent of predation risk at the monthly scale only, predation risk did influence fidelity during this time frame (rejecting P.2.1). In fact, close proximity to wolves or increased pack size increased female elk fidelity to monthly ranges. It seems that movements of female elk in RMNP at long temporal scales are primarily focussed

towards forage-rich areas, irrespective of predation risk. At shorter temporal scales (biweekly, weekly and especially daily) however, predation risk also influenced site fidelity (as expected by P.2.2) in a manner that suggests elk respond to predation risk by moving from high forage-abundance habitat to low forage-abundance habitat (Fig. 2; Figs. A3–A5, Online Resource 4) likely to avoid that detection by predators leads to an encounter and that an encounter leads to a chase (Gower et al. 2009). Indeed, when predation risk was high female elk frequently increased fidelity to low forage-abundant habitat such as wetlands and water bodies. In the absence of steep slopes in RMNP, such habitat types are considered effective escape terrain or safety refuges for elk during times of high predation risk (Paquet and Brook 2004). At the daily scale during autumn we found that predation risk interacted with both high and low forage-abundance habitat, indicative of a circular process in fine-scale movements in which female elk use escape terrain when predation risk is imminent but return to forage-rich sites once predation risk is reduced or absent. Generally, these results corroborate the notion that space-use patterns of prey are a result of dynamic predator-avoidance movements, which are evident most strongly at fine spatiotemporal scales (Mitchell and Lima 2002; Creel et al. 2005). Moreover, the observed switching in fidelity between high and low forage-abundant habitat as a function of predation risk is indicative of a trade-off between energetic requirements and safety, which seems a persistent feature in elk habitat selection (Kittle et al. 2008; Hebblewhite and Merrill 2009) and fine-scale movements (Creel et al. 2005; Frair et al. 2005).

We quantified temporal variation in movement patterns (i.e. site fidelity) for a spatially restricted, non-migratory population of elk. Clearly, elk also use other responses to balance demands for food and safety including changes in vigilance (Liley and Creel 2008), group size (Winnie and Creel 2007) or both (Childress and Lung 2003). Indeed, the attack abatement theory (Turner and Pitcher 1986) predicts that prey utilize a range of behavioural activities to minimize both encounters with predators (avoidance effect) and individual risk of depredation (dilution effect). It seems probable that each of the behavioural responses available to prey have additive or compensatory effects in the overall pursuit to avoid depredation. At present, however, it remains largely unknown how, and at which spatiotemporal scales, these responses interact, as well as their relative importance on prey dynamics (Creel et al. 2008). Our results show that female elk respond to wolf predation risk by alternating fidelity between high and low forage sites at the shortest (daily) temporal scale primarily. These findings agree with the idea that elk respond more strongly to risky times than risky places within their range (Creel et al. 2008). Furthermore, we found that this relation became less

obvious as the temporal scale of our analyses increased, and at the longest temporal scale (monthly) elk that ranged in areas close to wolves remained attached to these areas irrespective of the associated risk. This unexpected finding (P.2.1) may be explained if elk ranging in areas close to wolves at long temporal scales are able to dilute the risk by employing alternative antipredator behaviours such as increased vigilance or larger group sizes. We were unable to test this assumption as we lack vigilance or group size estimates at the detail of our GPS dataset. A more holistic investigation into the relative importance of multiple antipredator behaviours across spatiotemporal scales seems imperative to better understand predator–prey interactions, and moreover, how their combined effect influences population dynamics and ecosystem impacts (Creel 2011). Incorporating scale-dependence into this equation is crucial to capture the differences in activities performed at different spatial and temporal scales. For example, fine spatiotemporal scales typically involve foraging activities (Owen-Smith et al. 2010), which are influenced directly by local conditions such as ambient temperature (Rivrud et al. 2010; van Beest et al. 2011) and predation risk as shown here. Space-use patterns at increasingly larger scales incorporate multiple activities and life history needs (Bowyer and Kie 2006) and can be influenced differently and by other conditions than observed at fine scales.

The best-known studies regarding the spatial behaviour of elk in response to variation in forage abundance and predation risk by wolves come from YNP (Creel et al. 2005; Fortin et al. 2005; Gower et al. 2009; White et al. 2009). However, wolves were considered extirpated in Yellowstone by 1930 and reintroduced in 1995 (Bangs and Fritts 1996). The behavioural response of elk as observed in the newly restored YNP system should, therefore, be compared and validated against observations from other systems with established, long-term predator–prey coexistence, such as in RMNP, before being considered representative of widespread predator–prey dynamics. Our findings of short, fine-scale predator-avoidance movements with alternating overlap between forage-rich and forage-poor areas by elk has also been observed in YNP (Creel et al. 2005; Fortin et al. 2005; White et al. 2009). Most of the studies in YNP have focussed on elk-wolf interactions during winter. Here we have shown that in RMNP similar behavioural processes are apparent throughout the year and most clearly in autumn. However, the overall similarity in results from two separate systems with varying length of elk-wolf coexistence (RMNP and YNP) builds toward a general theory of elk–wolf predation dynamics that is less geographically limited. Furthermore, following declines in migratory behaviour in ungulate populations around the world (Berger 2004; Bolger et al. 2008) behavioural strategies employed within spatially restricted protected

areas and at fine temporal scales, such as observed in RMNP, are expected to become increasingly common.

For free-ranging large herbivores fidelity to sites where they survived in the past is likely the most effective strategy to ensure long-term fitness (Schaefer et al. 2000; Wolf et al. 2009). Our results corroborate recent findings that antipredator behaviour has the potential to directly influence the energy intake of elk (Christianson and Creel 2010) through a trade-off between forage and safety (Hebblewhite and Merrill 2009). The fitness cost of such antipredator responses in wild populations is a topic of increasing interest (Preisser et al. 2005), especially in elk-wolf systems, but the results remain equivocal. For example, Creel et al. (2011) showed that predation risk by wolves in YNP decreased pregnancy rates in elk, while White et al. (2011) did not detect any fitness consequences in elk following wolf predation risk. It is clear that to progress current theory of predation risk effects on ungulate (prey) behaviour and population dynamics more evidence is needed. Crucial in this process are the interactive effects between predation and forage at short temporal scales, as shown here, as well as the influence of other environmental conditions on animal behaviour such as climatic stochasticity (Tveraa et al. 2003; van Beest et al. 2011), and observations from a broad range of predator-prey systems with varying length of predator-prey coexistence.

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