

# Linking spring phenology with mechanistic models of host movement to predict disease transmission risk

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## Abstract

1. Disease models typically focus on temporal dynamics of infection, while often neglecting environmental processes that determine host movement. In many systems, however, temporal disease dynamics may be slow compared to the scale at which environmental conditions alter host space-use and accelerate disease transmission.
2. Using a mechanistic movement modelling approach, we made space-use predictions of a mobile host (elk [*Cervus Canadensis*] carrying the bacterial disease brucellosis) under environmental conditions that change daily and annually (e.g., plant phenology, snow depth), and we used these predictions to infer how spring phenology influences the risk of brucellosis transmission from elk (through aborted foetuses) to livestock in the Greater Yellowstone Ecosystem.
3. Using data from 288 female elk monitored with GPS collars, we fit step selection functions (SSFs) during the spring abortion season and then implemented a master equation approach to translate SSFs into predictions of daily elk distribution for five plausible winter weather scenarios (from a heavy snow, to an extreme winter drought year). We predicted abortion events by combining elk distributions with empirical estimates of daily abortion rates, spatially varying elk seroprevalence and elk population counts.
4. Our results reveal strong spatial variation in disease transmission risk at daily and annual scales that is strongly governed by variation in host movement in response to spring phenology. For example, in comparison with an average snow year, years with early snowmelt are predicted to have 64% of the abortions occurring on feedgrounds shift to occurring on mainly public lands, and to a lesser extent on private lands.
5. *Synthesis and applications.* Linking mechanistic models of host movement with disease dynamics leads to a novel bridge between movement and disease ecology. Our analysis framework offers new avenues for predicting disease spread, while providing managers tools to proactively mitigate risks posed by mobile disease

hosts. More broadly, we demonstrate how mechanistic movement models can provide predictions of ecological conditions that are consistent with climate change but may be more extreme than has been observed historically.

#### KEYWORDS

*Brucella abortus*, brucellosis, *Cervus canadensis*, disease transmission, elk, habitat selection, master equation, movement ecology, space-use, spring phenology, step selection function

## 1 | INTRODUCTION

Epidemiological models have traditionally focused on temporal aspects of disease dynamics (Diekman, Hesterbeak, & Britton, 2012; Keeling & Rohani, 2008), with less emphasis on spatial heterogeneity. Transmission is often determined by the movements of hosts and vectors, which are in turn influenced by environmental conditions. Yet, host movement is seldom linked to environmental conditions (Altizer, Bartel, & Han, 2011; Ostfeld, Glass, & Keesing, 2005). This is likely because of the human focus of much of the disease ecology field, and because movement models have been historically difficult to translate into mechanistic predictions of animal density (Moorcroft & Barnett, 2008) or spatially structured epidemiological systems (Keeling & Rohani, 2002). Incorporating host movement into disease models is particularly important for disease systems where temporal dynamics of infection and transmission act over a longer time-scale than factors that affect host movement such as food availability.

When studies do explicitly incorporate spatial heterogeneity, disease models such as the classic susceptible–infected–recovered (SIR) and related models (Diekman et al., 2012) tend to make simple assumptions about homogeneity in the spatial structure of the landscape and random movement of hosts and vectors (Keeling & Rohani, 2002). Nonetheless, even incorporating a relatively simple spatial component into disease models has led to novel predictions of disease dynamics (Benavides, Valderrama, & Streicker, 2016; Riley, 2007). For example, Smith, Lucey, Waller, Childs, and Real (2002) employed a stochastic spatial model to quantify spatial variation in rabies spread and found that large rivers act as semi-permeable barriers. In this case, including the spatial component illuminated how local transmission based on host movement and translocation of hosts by humans influence the spread of rabies (Smith et al., 2002). Further, including a dispersal kernel, based simply on how infectivity decreases with distance, has provided the baseline for spatial models of foot-and-mouth disease to identify how control efforts should be applied spatially (Keeling, 2005).

The field of animal ecology has a long history of assessing how environmental conditions drive individual movement and population spatial distribution (Guisan & Zimmermann, 2000; Manly, McDonald, Thomas, McDonald, & Erickson, 2002). Species distribution models (Elith & Leathwick, 2009) such as the resource selection function (RSF; Manly et al., 2002) are well-established and have been used to answer a plethora of applied and fundamental questions. The RSF is typically used to predict distributions based on static landscape variables or for

specific time periods (e.g., Losier et al., 2015), but such models do not account for the movement process between habitats as habitat quality changes through time (Merkle et al., 2016; van Moorter et al., 2013). In response to such constraints, mechanistic movement modelling has seen recent methodological advances, where animal space-use is now viewed as a pattern that is “scaled-up” mechanistically from the movement of individuals (Morales & Ellner, 2002). Advances in mechanistic movement modelling have included ecological diffusion models (Hefley, Hooten, Russell, Walsh, & Powell, 2017; Williams et al., 2017), as well as the step selection function (SSF; Fortin et al., 2005) and its translation into a probability density function of space use through stochastic simulations (Signer, Fieberg, & Avgar, 2017) or a master equation (Merkle, Potts, & Fortin, 2017; Potts, Bastille-Rousseau, Murray, Schaefer, & Lewis, 2014). These statistical methods identify the mechanisms driving animal movement, allowing a more explicit assessment of the influence of host movements on disease dynamics.

Despite the apparent usefulness of mechanistic movement models to epidemiological models, the two fields have only recently begun to merge (Garlick, Powell, Hooten, & McFarlane, 2011; Hefley et al., 2017). For instance, Hefley et al. (2017) use an ecological diffusion model to predict spatio-temporal dynamics of chronic wasting disease in white-tailed deer (*Odocoileus virginianus*). Yet, their model does not include individual-based animal movement data nor temporally varying variables that affect deer movement. We build on this work by fitting a mechanistic movement model of a mobile host monitored using GPS collars and then use a master equation approach to predict space use under environmental scenarios that change daily and annually (e.g., plant phenology, snow depth). We use these predictions to mechanistically link how weather patterns and forage availability (e.g., variability in snow depth and date/rate of spring vegetation green-up) influence spatio-temporal variation in disease transmission risk, via host movement.

We assessed spatio-temporal variation in brucellosis transmission risk from elk (*Cervus canadensis*) to domestic cattle (*Bos taurus*) in the Greater Yellowstone Ecosystem (GYE). Brucellosis is transmitted by contact with infected fetuses, placentas or birthing fluids (Cheville, McCullough, & Paulson, 1998); thus, it can be transmitted to cattle via comingling with elk between February and June, peaking March to May when most abortions occur (Cross et al., 2015). The potential transmission risk of brucellosis to cattle is a concern for livestock health, the sustainability of the ranching industry and tolerance for elk in the GYE (Bienen & Tabor, 2006; Kilpatrick, Gillin, & Daszak, 2009). Of particular

concern is that brucellosis seroprevalence in elk has increased in some areas of the GYE over the last 20 years (Cross et al., 2010), resulting in localized increased risk of transmission to cattle. To limit comingling of elk and cattle during the brucellosis transmission period in the Wyoming component of the GYE, winter supplemental feeding of elk is employed and ends between February and May during the abortion season (Cross, Edwards, Scurlock, Maichak, & Rogerson, 2007).

In the Mountain West, climate change is contributing to decreased snowpack, earlier snowmelt, and an increase in drought frequency and the rate of spring green-up (Bates, Kundzewicz, Wu, & Palutikof, 2008; Joyce, Haynes, White, & Barbour, 2005). Plant phenology strongly determines wild ungulate habitat use (Aikens et al., 2017) and selection (Merkle et al., 2016), including elk in our study area (Jones et al., 2014). To evaluate the influence of snow depth and vegetation phenology on brucellosis transmission risk, we predicted the spatio-temporal distribution of abortion events across five winter weather scenarios: observed low, average and heavy snow years; and two extreme early snowmelt or winter drought scenarios.

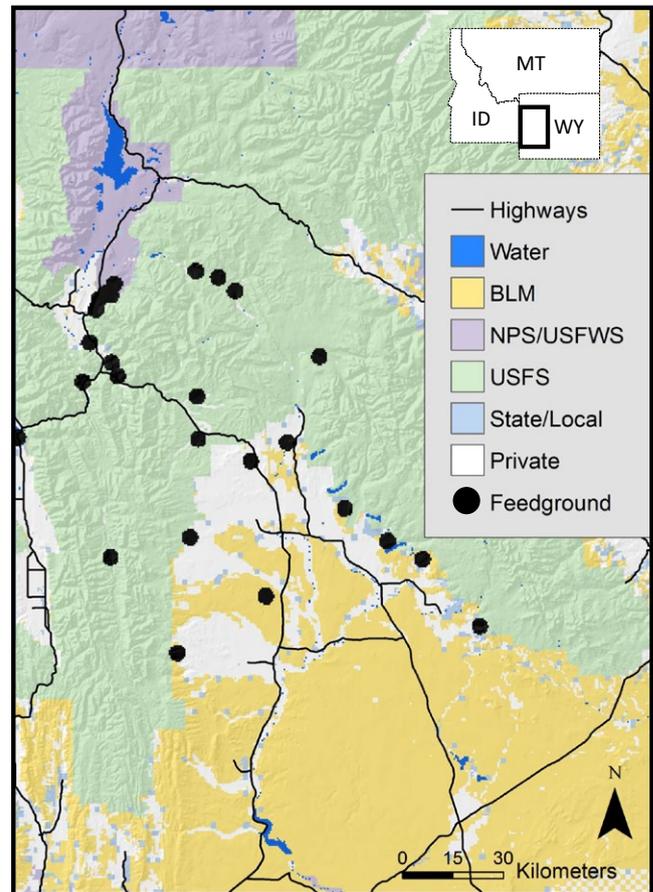
## 2 | MATERIALS AND METHODS

Our analysis consisted of four steps: (1) fit SSFs of elk movement in spring when brucellosis transmission risk is high; (2) derive elk distribution by employing a master equation approach based on the fitted SSFs across the aforementioned five weather scenarios; (3) multiply elk distribution predictions by adult and yearling female elk abundance, seroprevalence, pregnancy rate and daily probability of an abortion event (Cross et al., 2015); and (4) contrast the distribution of brucellosis transmission risk across different weather scenarios for public and private lands, which vary in the timing of livestock use.

### 2.1 | Study area and GPS collar data

Elevations in the Wyoming component of the GYE range from 1,700 m to 4,200 m. Land ownership is a mixture of private, state and local governments, Bureau of Land Management (BLM), U.S. Forest Service (USFS), U.S. Fish and Wildlife Service (USFWS) and U.S. National Park Service property (NPS; Figure 1). Sagebrush (*Artemisia* spp.) communities predominate at lower elevations (below 2,300 m), and transition to herbaceous meadows and lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) forests at mid-elevations (2,300 m to 2,900 m). Elevations above 2,900 m are predominated by herbaceous meadows, and spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) forests. The regional climate is characterized by long cold winters and relatively short warm summers (see Jones et al., 2014 for details).

We used GPS collar data from 288 adult and yearling female elk captured on 22 feedgrounds (range: 4–64 individual elk per feedground) from 2007 to 2014. Each individual elk was monitored for one to 2 years. Elk were captured in corral traps or chemically



**FIGURE 1** Study area in western Wyoming, USA, indicating the matrix of landownership and the locations of elk supplemental feedgrounds. Shading represents hillshade of elevation

immobilized from the ground with a dart containing 0.01 mg/kg carfentanil (ZooPharm, Windsor, CO, USA) and 0.1 mg/kg xylazine (Vedco, St. Joseph, MO, USA), and antagonized with 1 mg/kg naltrexone (ZooPharm, Windsor, CO, USA) and 2 mg/kg tolazoline (Lloyd Laboratories, Shenandoah, IA, USA). Although collars were programmed to collect locations every 30, 60 or 120 min, we rarefied the data to one location every four hours so that the probability of moving at least 250 m (the coarsest resolution of our GIS data) was >0.5.

### 2.2 | Derivation of animal distribution from a SSF

The SSF is a modelling approach equivalent to a biased correlated walk for estimating resource selection by mobile organisms (Duchesne, Fortin, & Rivest, 2015). The general form of the SSF is as follows:

$$f(x|y, s, \beta) = \frac{\Phi(x|y)\exp(\mathbf{Z}(x) \cdot \beta)}{\int_{I \in s} \Phi(I|y)\exp(\mathbf{Z}(I) \cdot \beta) dI} \quad (1)$$

where  $f(x|y, s, \beta)$  is the conditional probability of choosing location  $x$ , given the animal came from location  $y$ , and the 1:K available options  $s$ , where  $s = \{I_0, I_1, \dots, I_K\}$ .  $\Phi(x|y)$  is the probability, in a homogeneous

landscape, of moving from  $y$  to  $x$ .  $\mathbf{z}$  is a vector of environmental covariates, and  $\boldsymbol{\beta}$  is a vector of coefficients denoting the strength that each of the environmental covariates in  $\mathbf{Z}$  has on choice of  $s$  options. The denominator acts as a normalizing constant, ensuring that  $f(x|y, s, \boldsymbol{\beta})$  is a probability density function.

Predicting animal distribution from a SSF can be done through a master equation approach, where the population-level probability of use is derived using estimated SSF parameters (Potts et al., 2014). Given a landscape of grid cells (i.e., habitat patches), the master equation gives the probability density of a population at some time  $t + \Delta t$  as a function of both the probability density at time  $t$ , and the movement kernel. Denoting the probability that the population is in patch  $x$  at time  $t$  by  $u(x, t)$ , the master equation is

$$u(x, t + \Delta t) = \sum_{y \in \Omega} f(x|y, \Omega, \boldsymbol{\gamma}, \boldsymbol{\beta}) u(y, t) \quad (2)$$

where  $f(x|y, \Omega, \boldsymbol{\gamma}, \boldsymbol{\beta})$  is the movement kernel, and  $\Omega$  is the set of all habitat patches in the landscape.

At every iteration of the master equation, the movement kernel is calculated as the probability  $f(x|y, \Omega, \boldsymbol{\gamma}, \boldsymbol{\beta})$  of moving to location  $x$  (potential target patch) given being previously at  $y$  (the source patch),

$$f(x|y, \varepsilon, \boldsymbol{\gamma}, \boldsymbol{\beta}) = K^{-1} \Phi(x|y, \boldsymbol{\gamma}) f(x|y, \Omega, \boldsymbol{\beta}). \quad (3)$$

Here,  $\Phi(x|y, \boldsymbol{\gamma})$  is the step length distribution with  $\boldsymbol{\gamma}$  indicating the functional form of the distribution,  $f(x, y, \Omega, \boldsymbol{\beta})$  is the fitted SSF denoting the effect of the environment on the animal's movement or choice of a patch.  $K$  is a normalizing constant that ensures  $f(x|y, \Omega, \boldsymbol{\gamma}, \boldsymbol{\beta})$  integrates to 1 with respect to  $x$ , and  $\boldsymbol{\gamma}$  is a vector of parameters for the step length distribution (e.g., Weibull distribution).

## 2.3 | SSF development

We developed and fit a SSF for elk movement on and around each feedground (i.e., a feedground subpopulation) from the day supplemental feeding ended to 15 July (when brucellosis-induced abortion risk is predicted to be nearly zero; Cross et al., 2015). We fit SSFs separately for each feedground because we expected each subpopulation to behave differently based on previous analyses (Jones et al., 2014). For each four-hour step, we drew 10 potential target points originating from the known source point by simultaneously sampling step and turning angle distributions of all animals in the subpopulation. These 10 potential target points were identified as available and compared to the used target step.

Our SSFs included the following variables hypothesized to influence elk movement after supplemental feeding has ended: distance to any road (in km) including highways and jeep trails (30 m resolution, U.S. Department of Commerce, Bureau of the Census), elevation (30 m, U.S. Geological Survey National Elevation Dataset), snow depth (1 km, daily, Snow Data Assimilation System [SNODAS]), aspect (30 m, ranging from  $-1$  as southerly to  $1$  as northerly aspects), slope (30 m, in degrees), terrain position index (30 m, ranging from  $-50$  as valley bottoms to  $50$  as ridgetops, calculated as the difference

between the elevation of a cell and the mean elevation of its nearest 80 surrounding cells), per cent tree canopy cover (30 m, 2011 National Land Cover Database), overall productivity or biomass of a habitat patch each year calculated as the annual integrated Normalized Difference Vegetation Index (NDVI, 250-m resolution, MODIS data; Pettorelli et al., 2005), and the phenological stage of a habitat patch calculated as the daily NDVI value (scaled between 0 and 1) of a patch at the time the step was taken (250 m, calculated following the cleaning and smoothing methods of Merkle et al., 2016; Bischof et al., 2012).

## 2.4 | Fitting the SSF

We fit an SSF for each feedground subpopulation using conditional logistic regression, with each stratum identified as a used point and its paired 10 available target points. To reduce bias in estimated coefficients, particularly for variables that are strongly selected for, we included distance (in km) between the source and target points as a covariate to better represent heterogeneity in the availability domain at each step (Forester, Im, & Rathouz, 2009). Because of temporal autocorrelation and a lack of independence within an individual's movements, we calculated robust SE and 95% CI of parameters using generalized estimating equations (Craiu, Duchesne, & Fortin, 2008). All strata for a given individual and year were assigned a unique cluster in the SSFs. There was no collinearity among variables within fitted SSFs—Pearson correlations coefficients were  $<0.35$ , and variance inflation factors were  $<2.5$ . We validated the robustness of SSFs using fivefolds cross-validation repeated 100 times, following the framework developed by Fortin et al. (2009) for SSFs.

## 2.5 | Master equation parameters

We estimated the spatio-temporal distribution of elk around feedgrounds every 4 hr (i.e.,  $\Delta t$ ) on a 500 m grid of the study area by translating the SSFs for each feedground subpopulation into a master equation of space use. We chose a larger grid than the 250-m grid associated with NDVI data to reduce computation time for the calculations. We derived elk distribution from the day supplemental feeding ended to 15 July, using feeding end-dates and NDVI (i.e., green-up) data for 2010, 2012 and 2014, representing a low, average and heavy snowfall year, respectively (see Appendix S1 for details). We also derived elk distribution under two hypothetical climate change scenarios where spring green-up started, snow melt occurred, and supplemental feeding ended 14 and 28 days earlier than in the low snow year of 2010 (totalling five scenarios).

The starting distribution of elk was based on a fitted Weibull distribution of the distances that all elk GPS locations were from feedgrounds during the feeding season (January through April) for each feedground separately (Appendix S2). We specified the step length distribution  $\Phi(x|y, \boldsymbol{\gamma})$  as a Weibull distribution (shape = 0.88, scale = 0.47) fitted from all observed step lengths. The observed turning angle distribution was not included in the master equation because of the computational time and complexity involved. To verify

this did not alter our results, we refit our SSFs without taking into account turning angle distribution when sampling availability and found little difference in the estimated coefficients. A separate master equation was calculated for each feedground subpopulation using a domain  $\Omega$  of 25,600 pixels, representing a 40 km radius around each feedground. We validated predictions of the master equation and tested performance by comparing (1) mean predicted probability of elk use extracted for each observed elk relocation in 2010, 2012 and 2014, to mean predicted probability of elk use extracted for random points across the domain, (2) frequency of observed GPS collar locations falling within binned quantiles of predicted probability of elk use and (3) the expected per cent of locations (i.e., residuals) falling within equal bins of the probability of use broken down into four time periods (Appendix S5).

## 2.6 | Predicting disease transmission risk

To translate probability of elk use to disease transmission risk, we calculated the predicted number of abortion events  $a_{xt}$  per 500 m pixel  $x$ , per time step  $t$  (in days), for each of our five scenarios as

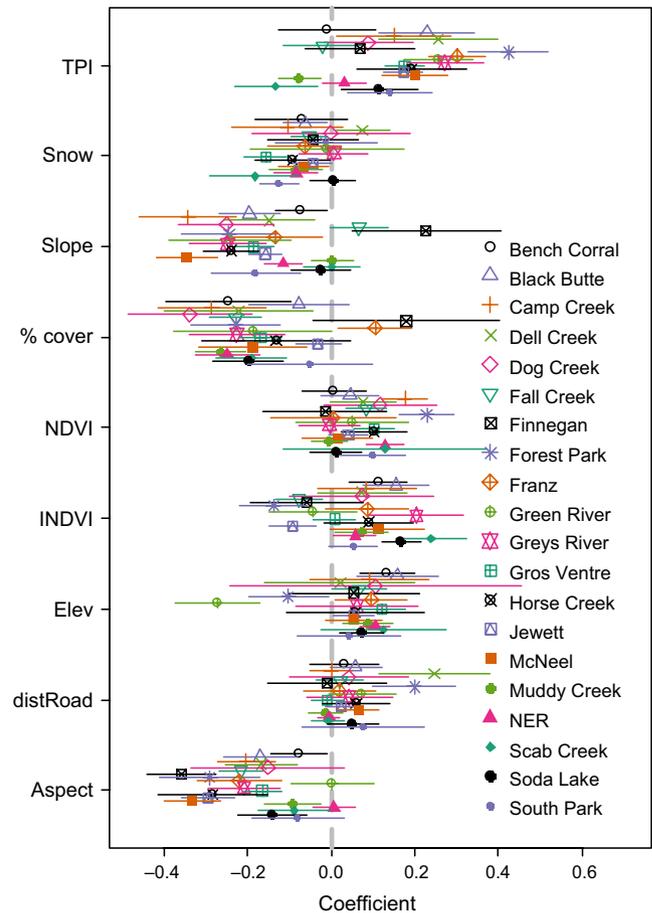
$$a_{xt} = u(x, t) \times N_x \times S_x \times y \times p(a_t) \quad (4)$$

where  $u(x, t)$  is the daily predicted probability of elk use,  $N_x$  is the number of female adult and yearling elk counted at each feedground (Appendix S3),  $S_x$  is the average brucellosis seroprevalence estimated on each feedground (Appendix S3),  $y$  is a mean pregnancy rate of 86.8% estimated based on ultrasonography of 871 adult and yearling female elk in winter across all feedgrounds from 1995 to 2012 (Wyoming Game and Fish Department, Unpubl. data), and  $p(a_t)$  is the predicted daily probability of aborting given an individual is seropositive and pregnant (empirically estimated from Cross et al., 2015). The predicted number of abortion events  $a_{xt}$  per 500 m pixel was calculated for each subpopulation separately and then summed together across the entire study area.

## 3 | RESULTS

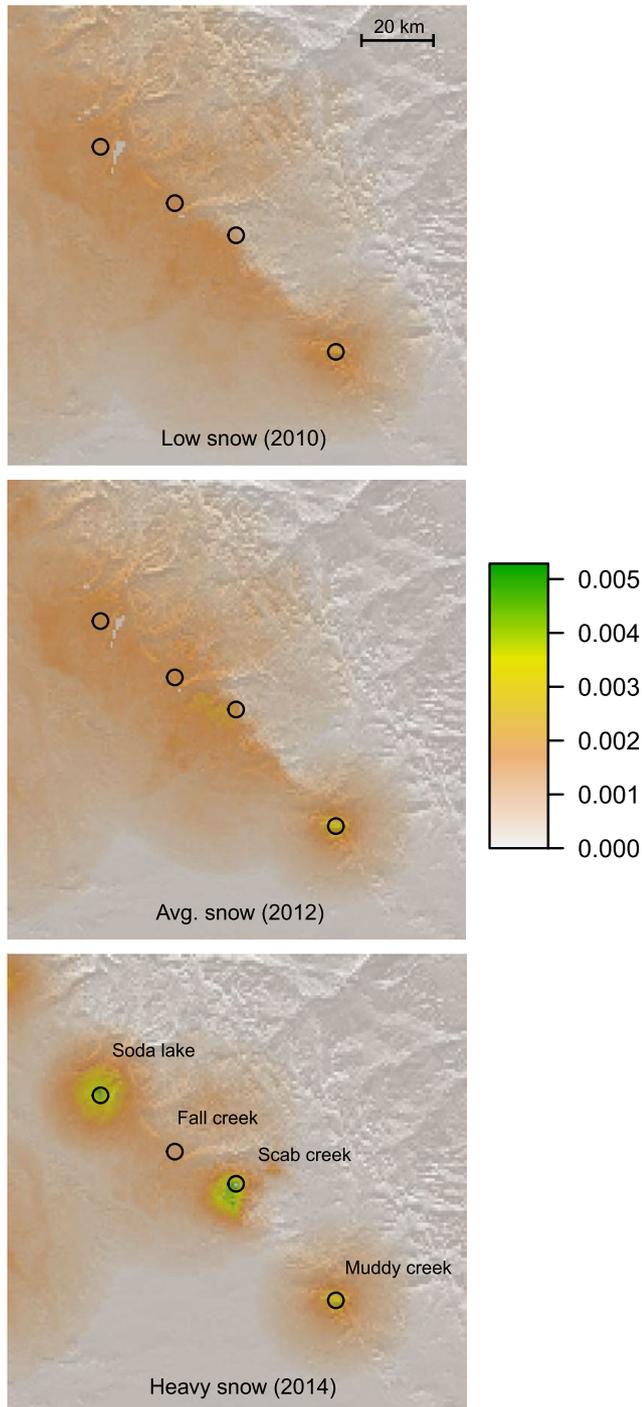
Mean date when supplemental feeding ended across all feedgrounds was 21 March ( $SD = 22$  days) in 2010, 26 March ( $SD = 21$ ) in 2012 and 12 April ( $SD = 25$ ) in 2014, representing >3-week variation from low to heavy snowfall years. After elk left feedgrounds, they tended to select habitat patches that were on south facing gentle slopes, farther away from roads, at higher elevations, with higher annual integrated NDVI (i.e., surrogate for patch quality or biomass), with higher daily NDVI (i.e., surrogate for phenology stage), with lower canopy cover, and with a higher terrain position index (i.e., selecting ridges over valleys). Nevertheless, there was variation in parameter estimates among feedground subpopulations (Figure 2). Our SSFs were robust to k-folds cross-validation, with good-to-excellent predictive ability depending on feedground subpopulation (Appendix S4).

Using the SSF for each feedground subpopulation, we predicted the probability of elk use per 500 m pixel per day across



**FIGURE 2** Standardized coefficient estimates (with 95% CI denoted by lines) for step selection functions fit for elk subpopulations ( $n = 288$  individuals) occurring across 22 feedgrounds in Wyoming during spring, 2007–2014. Variables included were terrain position index (TPI), snow depth (Snow), slope, per cent tree cover (% cover), daily NDVI value (NDVI), integrated NDVI (INDVI), elevation (Elev), distance to road (distRoad) and aspect

the five weather scenarios. Based on three validation procedures, our model predicted elk GPS collar relocation data well (Appendix S5). The predicted number of abortion events per 500 m pixel, per day across the landscape ranged from 0 to a maximum of 0.03. We estimated that c. 712 abortion events occurred per year across the study area. Due to a combination of elk density and brucellosis seroprevalence, the number of cumulative abortions per year varied widely among feedground subpopulations. The most abortions occurred on and around the National Elk Refuge, Gros Ventre, and Horse Creek feedgrounds (217, 77 and 60, respectively), and the least occurred on and around the Finnegan and Fall Creek feedgrounds (6 and 7, respectively; Appendix S6). Most abortions occurred on USFS lands and there was considerable variation in the spatial distribution of brucellosis transmission risk among scenarios (See Figure 3 for an example). In general, during heavy snow years, elk used feedgrounds later in the season, concentrating brucellosis transmission risk on feedgrounds. In contrast, during low snow years, and scenarios where supplemental feeding ended, and



**FIGURE 3** Predicted number of abortion events on 10 April per 500 m pixel on the south-western slopes of the Wind River mountain range, Wyoming, including four feedgrounds (denoted by open circles) for 2010 (low snow year), 2012 (average snowfall year) and 2014 (heavy snowfall year). Predicted number of abortion events derived from multiplying the predicted probability of elk use by adult and yearling female abundance, brucellosis seroprevalence, pregnancy rate and the daily probability of an abortion event. Shading represents hillshade of elevation

green-up occurred, up to 4 weeks earlier in the year, elk left the feedgrounds earlier, spreading abortions more widely across the landscape (Figure 3).

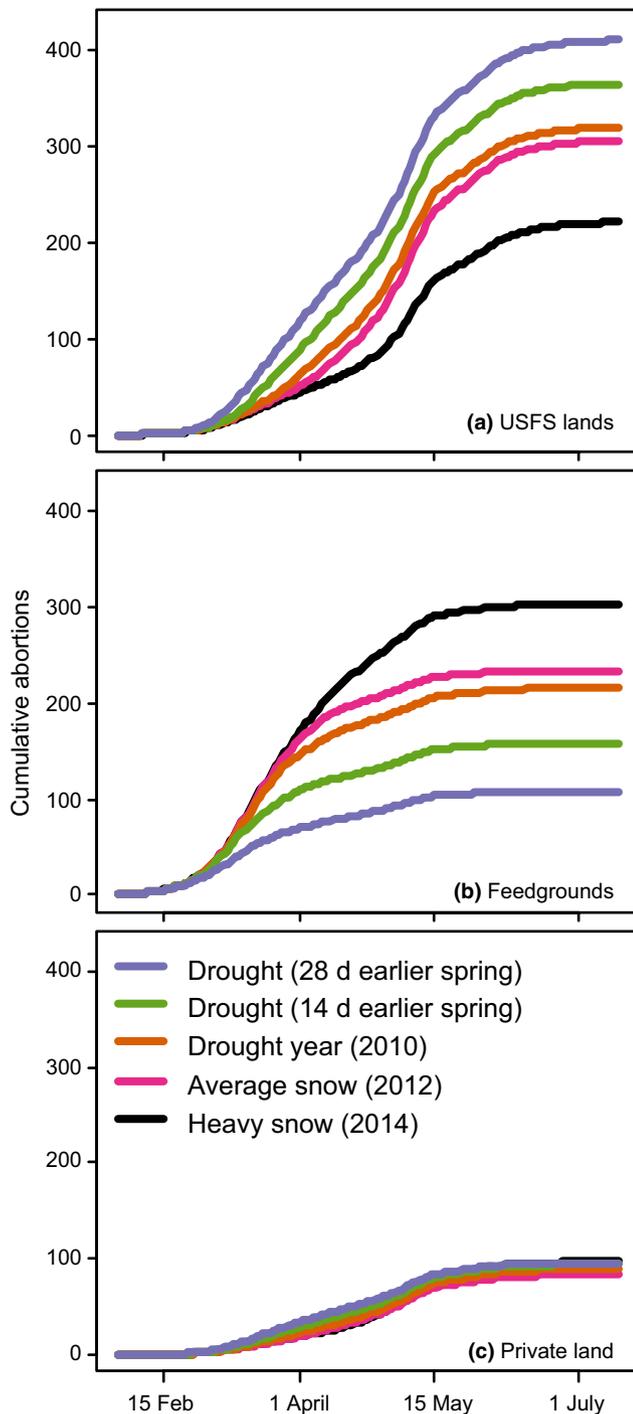
We predicted that during the average snow year of 2012, c. 307 (43%) abortions occurred on USFS lands, 234 (33%) within 2.5 km of feedgrounds, 84 (12%) on private land, 30 (3%) on BLM lands, 49 (7%) on USFWS/NPS lands and <9 (1%) occurred across state and local government lands (Appendix S7). However, these proportions varied among the five weather and supplemental feeding end-date scenarios. From a heavy snow year to a 28-day early snowmelt or winter drought year, the number of abortions on feedgrounds decreased by 64% (from 302 to 108), whereas the number of abortions on USFS increased by 85% (from 221 to 411). Abortions on private lands only slightly decreased from 97 to 96 and abortions on USFWS/NPS lands only slightly increased from 52 to 54. Collectively, these results suggest that as elk leave feedgrounds earlier during early snowmelt or winter drought years, abortions occurred more on USFS lands without detectable change on other land ownership types (Figure 4).

Changes in the spatial distribution of elk abortions were more pronounced earlier in the abortion season (March and April), where we predicted the majority of elk abortions to occur on feedgrounds during heavy snow years, and the majority of abortions to occur on USFS lands during early snowmelt and winter drought years (Figure 5; Appendix S7). Aune, Rhyan, Russell, Roffe, and Corso (2012) reported that brucellosis can persist in the environment around a foetus up to 26 days post-abortion. Because most grazing allotments on USFS lands adjacent to elk feedgrounds open on 15 June, 19 May can be considered the cut-off for abortions with a high risk of brucellosis transmission from elk to cattle. After 19 May during the average snow year, c. 64 abortions (9% of all abortions) were predicted to occur on USFS lands, 13 (2%) to occur on private lands and 7 (1%) to occur on feedgrounds. However, there was less variation in these numbers across the five scenarios (e.g., abortions on USFS lands varied from 55 to 70 after 19 May). Appendix S8 details the spatio-temporal distribution of abortions across the five scenarios by feedground subpopulation.

## 4 | DISCUSSION

Our work connects variation in weather and plant phenology with disease transmission risk via host movement at the landscape scale. We found that c. 700 abortion events occur per year in our study region and that, as expected, weather and phenology—by influencing elk movement—alter the spatial distribution of springtime abortion events and thus brucellosis transmission risk. During early snowmelt or winter drought years, up to 190 more abortions may occur within grazing allotments on USFS than in heavy snow years (an increase of 85%). Meanwhile, the risk of brucellosis transmission on private lands was relatively unaffected by annual weather patterns.

Our mechanistic predictions of brucellosis transmission risk make three contributions to understanding disease transmission. First, we predicted population-level spatial distribution based on individual movement rules and environmental variables that vary both spatially and temporally. Such predictive capacity is rare (but see Merkle, Potts, & Fortin, 2017), yet as rapid environmental change may result in significant changes to global ecosystems (Barnosky et al., 2012), it is



**FIGURE 4** Predicted number of abortion events per year occurring on US Forest Service (USFS) lands (a), within 2.5 km of feedgrounds (b), and on private lands (c) during the heavy snow year of 2014, average snow year of 2012, low snow year of 2010, as well as a 14- and 28-day early snowmelt or winter drought year in Wyoming. Cumulative abortion events were derived from multiplying the predicted probability of elk use by adult and yearling female abundance, brucellosis seroprevalence, pregnancy rate and the daily probability of an abortion event

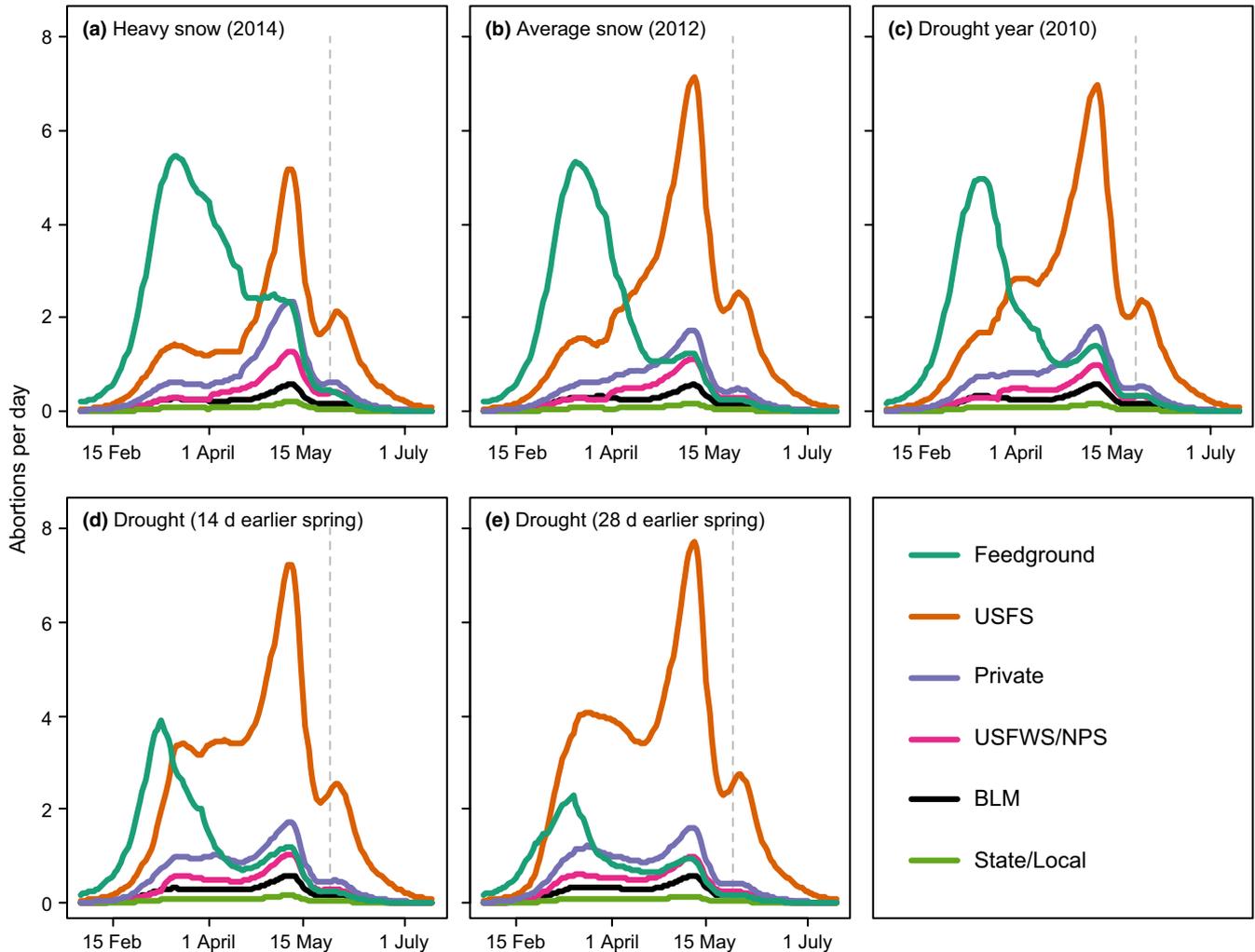
imperative that we employ these mechanistic or process-based models to predict future ecological states that may diverge from past conditions (Gustafson, 2013). Secondly, we have incorporated a spatially

explicit model of host behaviour into predictions of disease transmission, whereby we predicted disease transmission risk based on the underlying factors that influence host movement. Such an explicit bridge between movement and disease ecology is rare (Altizer et al., 2011) and, based on our results, can result in useful predictions of disease dynamics in both space and time. Finally, we provide a comprehensive mapping tool for identifying the spatio-temporal risk of brucellosis transmission across a large landscape. By projecting where and when hundreds of abortion events occur each year across varying snow and green-up dynamics, we provide predictions of how spatial brucellosis risk will change within and among years.

In this study, we borrow spatial modelling frameworks from animal ecology and apply them to a chronic disease of wildlife and livestock. Brucellosis transmission occurs during spring when animals leave winter range and migrate to higher elevations (Cross et al., 2015; Jones et al., 2014), and our results demonstrate how annual weather variability can influence the phenology of host movement and thus the spatial dynamics of brucellosis transmission risk (Figures 4 and 5). As climate change continues to alter weather patterns, host movements and spatial distribution will inevitably change, resulting in novel disease dynamics in the future. Predictive models, such as the SSF (Fortin et al., 2005) and master equation (Potts et al., 2014) frameworks, represent an advancement in how animal distribution is predicted in space and time, and helps researchers and managers assess how climate change might alter disease dynamics or other ecological dynamics in unpredictable ways.

Our model, however, did not include a temporal transmission component, and as a result, does not allow for predictions of disease dynamics across consecutive years. For instance, based upon our spatial within-year analyses, we found that c. 300 abortion events could occur on feedgrounds during a heavy snow year compared to just over 100 in an early snowmelt or winter drought year. This high number of abortion events occurring on feedgrounds during heavy snow years is likely to enhance disease transmission within the elk population (Creech et al., 2012; Cross et al., 2010; Maichak et al., 2009), which may alter seroprevalence in years following heavy winter snow. Coupling mechanistic models of host movement with temporal models of transmission is an obvious next step in this system and within the broader disease ecology field.

Our modelling framework provides information for researchers and managers to prioritize management and conservation actions and identify where and when their implementation would be most effective. In our case, managing brucellosis comingling risk between elk and cattle during the abortion season is the main management option for wildlife and livestock managers (Kilpatrick et al., 2009; Proffitt et al., 2011), because other available options to eradicate disease in wildlife populations (i.e., test and slaughter, whole-herd culling and vaccination) do not appear to work, or are not logistically or politically possible for brucellosis management in the GYE (Bienen & Tabor, 2006). Available management actions include hazing elk away from cattle feeding areas, abandoning grazing allotments with high risk of comingling, and altering cattle turnout dates after risk of brucellosis transmission has subsided. Our maps of the number of abortion events



**FIGURE 5** Predicted number of abortion events per day across landownership in Wyoming based on green-up and supplemental feeding end-date data for the heavy snow year of 2014 (a), average snow year of 2012 (b), low snow year of 2010 (c), as well as a 14- (d) and 28-day (e) early snowmelt or winter drought year. Vertical dotted line represents 19 May—the predominant turnout date on US Forest Service lands (15 June) minus 26 days to take into account how long brucellosis can persist after an abortion event. Number of abortion events was calculated by multiplying the predicted probability of elk use by adult and yearling female abundance, brucellosis seroprevalence, pregnancy rate and the daily probability of an abortion event

per day provide the metrics to evaluate successful implementation of these management actions. For example, cattle grazing allotments on USFS lands near feedgrounds currently do not open for grazing until 15 June to minimize brucellosis transmission risk. Yet, our work suggests that there is still some risk of brucellosis transmission after this date (Figure 5). Given how elk movements in spring vary widely (up to a month or more) due to spring phenology (Figure 3), livestock regulatory health officials and cattle producers can use our risk assessment maps to assess the best turnout date both on an allotment-by-allotment basis, and on a year-to-year basis as snow conditions vary.

Our results suggest that regional variation in brucellosis transmission risk—due to variation in elk density and brucellosis seroprevalence across feedground subpopulations (Appendix S6)—is larger than that caused by annual weather variability. For instance, general trends in brucellosis transmission risk for each weather scenario are fairly similar among feedground subpopulations, and weather

variability does not affect transmission risk differently among feedground subpopulations (Appendix S8). Thus, although low snow years result in fewer abortions on feedgrounds and more on USFS and private lands, it is most important for wildlife and livestock managers to focus on allocating management resources to specific areas with the highest brucellosis transmission risk. Further, we found relatively little difference in the predicted number of abortion events on private lands across the weather scenarios (Figure 4c). These results suggest that although cattle on private lands have some risk of contacting aborted elk foetuses, adjusting cattle turnout dates on USFS lands should result in the largest reductions in brucellosis transmission risk.

We assumed that the predictor variables of the SSF, elk population size, seroprevalence, abortion timing, and pregnancy rates were all measured without error. In addition, we did not assess the estimation uncertainty in the space-use predictions. Thus, our inference should

be used with caution as our predictions do not include confidence intervals. Quantifying error in our predictions is an important avenue for further work (Hefley et al., 2017) as it would highlight to both researchers and managers where research efforts could be targeted to minimize the uncertainty in predictions of brucellosis transmission risk in the most cost-effective manner. Uncertainty could be estimated by drawing different parameter sets given the mean and variance of parameter estimates from the SSF and then deriving the resulting space use. Error estimates could then be compiled on a cell-by-cell basis so that prediction error could be assessed in both space and time. Such an exercise would be computationally challenging, but is likely to be feasible in the foreseeable future. Nonetheless, we examined how well the overall mean space-use predictions represent the observed movement patterns of collared elk and found that our space-use predictions accurately forecasted the location of observed elk GPS locations (Appendix S5).

In this work, we have bridged the movement and disease ecology fields so that spatio-temporal predictions of future ecological states are possible. Coupling predictions of host space-use with disease dynamics at the individual and population scale provided a new link between mechanistic movement models and predictions of disease transmission risk. Predicting such variation in host distribution and disease transmission risk provides a means to test predictions of how small-scale environmental changes can result in large-scale changes in animal distribution and disease spread, while enabling managers to identify where proactive management can mitigate risks posed by mobile disease hosts.

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## AUTHORS' CONTRIBUTIONS

J.A.M., P.C.C. and M.J.K. conceived the study. J.A.M. performed all analyses. Data were collected by P.C.C., B.M.S., E.K.C., A.B.C., S.R.D. and M.J.K. J.A.M. wrote the manuscript, and all authors contributed to revisions and approved its final version for publication.

## DATA ACCESSIBILITY

Data available from ScienceBase. <https://doi.org/10.5066/f7474803> (Merkle, Cross, et al., 2017).

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## REFERENCES

- Aikens, E. O., Kauffman, M. J., Merkle, J. A., Dwinell, S. P. H., Frailick, G. L., & Monteith, K. L. (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters*, 20, 741–750.
- Altizer, S., Bartel, R., & Han, B. A. (2011). Animal migration and infectious disease risk. *Science*, 331, 296–302.
- Aune, K., Rhyan, J. C., Russell, R., Roffe, T. J., & Corso, B. (2012). Environmental persistence of *Brucella abortus* in the Greater Yellowstone Area. *The Journal of Wildlife Management*, 76, 253–261.
- Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., ... Marquet, P. A. (2012). Approaching a state shift in Earth's biosphere. *Nature*, 486, 52–58.
- Bates, B. C., Kundzewicz, Z. W., Wu, S., & Palutikof, J. P. (2008). Climate change and water. In *Technical paper of the Intergovernmental Panel on Climate Change (IPCC)*. Geneva: Secretariat.
- Benavides, J. A., Valderrama, W., & Streicker, D. G. (2016). Spatial expansions and travelling waves of rabies in vampire bats. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160328.
- Bienen, L., & Tabor, G. (2006). Applying an ecosystem approach to brucellosis control: Can an old conflict between wildlife and agriculture be successfully managed? *Frontiers in Ecology and the Environment*, 4, 319–327.
- Bischof, R., Egil Loe, L., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *American Naturalist*, 180, 407–424.
- Cheville, N. F., McCullough, D. R., & Paulson, L. R. (1998). *Brucellosis in the greater Yellowstone area*. Washington, DC, USA: National Academies Press.
- Craiu, R. V., Duchesne, T., & Fortin, D. (2008). Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal*, 50, 97–109.
- Creech, T. G., Cross, P. C., Scurlock, B. M., Maichak, E. J., Rogerson, J. D., Henningsen, J. C., & Creel, S. (2012). Effects of low-density feeding on elk-fetus contact rates on Wyoming feedgrounds. *The Journal of Wildlife Management*, 76, 877–886.
- Cross, P., Cole, E., Dobson, A., Edwards, W., Hamlin, K., Luikart, G., ... White, P. (2010). Probable causes of increasing brucellosis in free-ranging elk of the Greater Yellowstone Ecosystem. *Ecological Applications*, 20, 278–288.
- Cross, P. C., Edwards, W. H., Scurlock, B. M., Maichak, E. J., & Rogerson, J. D. (2007). Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications*, 17, 957–964.
- Cross, P. C., Maichak, E. J., Rogerson, J. D., Irvine, K. M., Jones, J. D., Heisey, D. M., ... Scurlock, B. M. (2015). Estimating the phenology of elk brucellosis transmission with hierarchical models of cause-specific and baseline hazards. *The Journal of Wildlife Management*, 79, 739–748.
- Diekman, O., Hesterbeak, H., & Britton, T. (2012). *Mathematical tools for understanding infectious disease dynamics*. Princeton, NJ, USA: Princeton University Press.
- Duchesne, T., Fortin, D., & Rivest, L.-P. (2015). Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. *PLoS ONE*, 10, e0122947.
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677.

- Forester, J. D., Im, H. K., & Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. *Ecology*, *90*, 3554–3565.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*, 1320–1330.
- Fortin, D., Fortin, M. E., Beyer, H. L., Duchesne, T., Courant, S., & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology*, *90*, 2480–2490.
- Garlick, M. J., Powell, J. A., Hooten, M. B., & McFarlane, L. R. (2011). Homogenization of large-scale movement models in ecology. *Bulletin of Mathematical Biology*, *73*, 2088–2108.
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.
- Gustafson, E. J. (2013). When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology*, *28*, 1429–1437.
- Hefley, T. J., Hooten, M. B., Russell, R. E., Walsh, D. P., & Powell, J. A. (2017). When mechanism matters: Bayesian forecasting using models of ecological diffusion. *Ecology Letters*, *20*, 640–650.
- Jones, J. D., Kauffman, M. J., Monteith, K. L., Scurlock, B. M., Albeke, S. E., & Cross, P. C. (2014). Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications*, *24*, 1769–1779.
- Joyce, L., Haynes, R., White, R., & Barbour, R. J. (2005). Bringing climate change into natural resource management: *Proceedings. Gen. Tech. Rep. PNW-GTR-706*, pp. 150. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Keeling, M. J. (2005). Models of foot-and-mouth disease. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*, 1195–1202.
- Keeling, M. J., & Rohani, P. (2002). Estimating spatial coupling in epidemiological systems: A mechanistic approach. *Ecology Letters*, *5*, 20–29.
- Keeling, M. J., & Rohani, P. (2008). *Modeling infectious diseases in humans and animals*. Princeton, USA: Princeton University Press.
- Kilpatrick, A. M., Gillin, C. M., & Daszak, P. (2009). Wildlife-livestock conflict: The risk of pathogen transmission from bison to cattle outside Yellowstone National Park. *Journal of Applied Ecology*, *46*, 476–485.
- Losier, C. L., Couturier, S., St-Laurent, M. H., Drapeau, P., Dussault, C., Rudolph, T., ... Fortin, D. (2015). Adjustments in habitat selection to changing availability induce fitness costs for a threatened ungulate. *Journal of Applied Ecology*, *52*, 496–504.
- Maichak, E. J., Scurlock, B. M., Rogerson, J. D., Meadows, L. L., Barbknecht, A. E., Edwards, W. H., & Cross, P. C. (2009). Effects of management, behavior, and scavenging on risk of brucellosis transmission in elk of western Wyoming. *Journal of Wildlife Diseases*, *45*, 398–410.
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals*, (2nd ed.). Dordrecht, the Netherlands: Kluwer Academic Publishers.
- Merkle, J. A., Cross, P. C., Scurlock, B. M., Cole, E. K., Courtemanch, A. B., Dewey, S. R., ... Szcudronski, K. E. (2017). Elk movement and predicted number of brucellosis-induced abortion events in the southern Greater Yellowstone Ecosystem (1993-2015): U.S. Geological Survey data release, <https://doi.org/10.5066/f7474803>
- Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., ... Kauffman, M. J. (2016). Large herbivores surf waves of green-up in spring. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20160456.
- Merkle, J. A., Potts, J. R., & Fortin, D. (2017). Energy benefits and emergent space use patterns of an empirically parameterized model of memory-based patch selection. *Oikos*, *126*, 185–195.
- Moorcroft, P. R., & Barnett, A. (2008). Mechanistic home range models and resource selection analysis: A reconciliation and unification. *Ecology*, *89*, 1112–1119.
- Morales, J. M., & Ellner, S. P. (2002). Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology*, *83*, 2240–2247.
- Ostfeld, R. S., Glass, G. E., & Keesing, F. (2005). Spatial epidemiology: An emerging (or re-emerging) discipline. *Trends in Ecology & Evolution*, *20*, 328–336.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, *20*, 503–510.
- Potts, J. R., Bastille-Rousseau, G., Murray, D. L., Schaefer, J. A., & Lewis, M. A. (2014). Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. *Methods in Ecology and Evolution*, *5*, 253–262.
- Proffitt, K. M., Gude, J. A., Hamlin, K. L., Garrott, R. A., Cunningham, J. A., & Grigg, J. L. (2011). Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *Journal of Applied Ecology*, *48*, 471–478.
- Riley, S. (2007). Large-scale spatial-transmission models of infectious disease. *Science*, *316*, 1298–1301.
- Signer, J., Fieberg, J., & Avgar, T. (2017). Estimating utilization distributions from fitted step-selection functions. *Ecosphere*, *8*, e01771.
- Smith, D. L., Lucey, B., Waller, L. A., Childs, J. E., & Real, L. A. (2002). Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America of the United States of America*, *99*, 3668–3672.
- van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., & Sæther, B. E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, *82*, 770–780.
- Williams, P. J., Hooten, M. B., Womble, J. N., Esslinger, G. G., Bower, M. R., & Hefley, T. J. (2017). An integrated data model to estimate spatiotemporal occupancy, abundance, and colonization dynamics. *Ecology*, *98*, 328–336.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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