Received: 20 June 2019 | Accepted: 5 February 2020

DOI: 10.1111/1365-2656.13199

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Territoriality drives preemptive habitat selection in recovering wolves: Implications for carnivore conservation

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Funding information
Michigan Technological University Ecosystem Science Center; Michigan Department of Natural Resources, Grant/Award Number: #751B430037; DeVlieg Foundation; National Science Foundation, Grant/Award Number: ID#1545611 and ID#1556676; Pittman-Robertson

Handling Editor: Eric Vander Wal

Abstract

1. According to the ideal-free distribution (IFD), individuals within a population are free to select habitats that maximize their chances of success. Assuming knowledge of habitat quality, the IFD predicts that average fitness will be approximately equal among individuals and between habitats, while density varies, implying that habitat selection will be density dependent. Populations are often assumed to follow an IFD, although this assumption is rarely tested with empirical data, and may be incorrect when territoriality indicates habitat selection tactics that deviate from the IFD (e.g. ideal-despotic distribution or ideal-preemptive distribution).
2. When territoriality influences habitat selection, species' density will not directly reflect components of fitness such as reproductive success or survival. In such cases, assuming an IFD can lead to false conclusions about habitat quality. We tested theoretical models of density-dependent habitat selection on a species known to exhibit territorial behaviour in order to determine whether commonly applied habitat models are appropriate under these circumstances.
3. We combined long-term radiotelemetry and census data from grey wolves *Canis lupus* in the Upper Peninsula of Michigan, USA to relate spatiotemporal variability in wolf density to underlying classifications of habitat within a hierarchical state-space modelling framework. We then iteratively applied isodar analysis to evaluate which distribution of habitat selection best described this recolonizing wolf population.
4. The wolf population in our study expanded by >1,000% during our study (~50 to >600 individuals), and density-dependent habitat selection was most consistent with the ideal-preemptive distribution, as opposed to the ideal-free or ideal-despotic alternatives.
5. Population density of terrestrial carnivores may not be positively correlated with the fitness value of their habitats, and density-dependent habitat selection patterns may help to explain complex predator–prey dynamics and cascading indirect effects. Source–sink population dynamics appear likely when species exhibit rapid growth and occupy interspersed habitats of contrasting quality. These conditions are likely and have implications for large carnivores in many systems, such as areas in North America and Europe where large predator species are currently recolonizing their former ranges.

KEYWORDS
anthropogenic mortality, apex predators, density-dependent habitat selection, isodar, predator–prey, rewilding, source–sink population dynamics, trophic cascades

1 | INTRODUCTION

Understanding the mechanisms underlying habitat selection is of fundamental importance to animal ecology because of their implications for population dynamics and the conservation of species. Habitat selection is expected to be functionally dependent on conspecific density when animals distribute themselves in a way that maximizes fitness and minimizes competition for resources (McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010; Morris, 1988). Studies of habitat selection often assume that animals within a population follow an ideal-free distribution (IFD) of space use. According to the IFD, individuals within a population are free to select habitats that maximize their chances of success. Assuming ideal knowledge of habitat quality, the IFD predicts that average fitness will be approximately equal on average among individuals, and between habitats, while density varies (density-dependent habitat selection; Fretwell & Lucas, 1969; Morris, 1988). Support for the IFD has been indicated in several systems (e.g. Haugen et al., 2006; Morris, 2003a; Quaintenne, Gils, Bocher, Dekinga, & Piersma, 2011; van Beest, McLoughlin, Vander Wal, & Brook, 2014), but deviations from the IFD are also common due to cognitive, resource and movement limitations, and competitive interactions (reviewed in Street, Erovenko, & Rowell, 2018). In comparison, less is known about theoretical distributions where animals either compete directly for territory (ideal-despotic or ideal-dominant distribution [IDD]; Beckman & Berger, 2003; Fretwell & Lucas, 1969; Oro, 2008) or preemptively occupy the best available habitat sites (ideal-preemptive distribution [IPD; Pulliam & Danielson, 1991]). In the latter situation, the relationship between fitness, density and habitat quality becomes more complex, such that density no longer reliably predicts differences in fitness among habitat classes (Morris, 1994). Direct tests of the distributions that best describe territorial species are rare because adequate data are uncommon (but see Edwards, Preu, Crealy, & Shakeshaft, 2002; Knight, Morris, & Haedrich, 2008), so it is often unclear whether empirical evidence supports theoretical expectations (Haché, Villard, & Bayne, 2013; McLoughlin et al., 2006; Morris, 2003a, 2003b).

Isodar theory is a framework for testing theoretical habitat distributions and can reveal influences of density dependence on habitat selection patterns (Morris, 2003a). A habitat isodar is generated by separating a population's geographic distribution into distinguishable classes (e.g. habitat A vs. habitat B), where the population's density can be estimated in each class (Morris, 1987, 1988, 1994). More specifically, an isodar is constructed by repeatedly gathering estimates of density in each class over time and plotting paired densities in habitat A versus habitat B. The isodar can take a variety of linear or nonlinear shapes, which may imply an underlying habitat selection distribution such as IFD, IDD or IPD, and can reveal important insights about animal behaviours and population dynamics (McLoughlin et al., 2010; Morris, 1994, 2003a). Under the IFD, if two habitats differ in suitability, then fitness declines as a function of density in both habitats but the average density in one habitat is consistently higher than the other (Figure 1a; Morris, 1988, 1994). According to this model, the inferior habitat should be unoccupied when density is low in the superior habitat (the intercept in Figure 1b; McLoughlin et al., 2010; Morris, 1988, 1994).

A linear isodar often suggests an IFD, but does not preclude the IDD (Morris, 1994; Mosser, Fryxell, Eberly, & Packer, 2009). Under the IDD, competitive exclusion and interference by more dominant or experienced individuals reduces potential habitat quality for subordinates, such that an alternative lower density habitat might have equivalent fitness benefits (Morris, 1994). Interference from dominant, territorial individuals has the effect of reducing perceived fitness for subordinates (dashed lines in Figure 1c), and the adjustment to fitness caused by territorial interference is indicated by a mismatch between true and perceived habitat quality (Figure 1c; McLoughlin et al., 2010; Morris, 2003b). Accordingly, the IDD predicts unequal fitness between the two habitat classes for a given density (Morris, 1994). Under the IDD, an isodar can take either a straight-line shape (additive competition) or follow a logarithmic function (multiplicative competition; Knight et al., 2008; Morris, 1994). Because a linear isodar may still be observed under an IDD (Figure 1d), other evidence may be needed to distinguish an IDD from an IFD, such as observed differences in survival, reproduction or growth rates between habitat classes. The IPD model offers an interesting alternative hypothesis to IDD (Figure 1e,f). Under the IPD, access to a site is determined by first arrival and selection of the best available site. Whereas an IDD might produce a curvilinear isodar (fit to log-transformed densities; Knight et al., 2008; Morris, 1994, 2003a), the IPD often results in a specific nonlinear shape (Figure 1f) that distinguishes it from the IFD and IDD and likely indicates preemptive habitat selection (Morris, 1994; Pulliam & Danielson, 1991). Additionally, the specific shape of a nonlinear isodar can imply patterns that might otherwise go undetected. For example, an S-shaped (sigmoidal) isodar may reveal differences in the variance of site quality between two habitats, whereas an asymptotic isodar suggests saturation of a limited number of high quality sites that can result in niche-shifts or switching of preferred habitats (Morris, 1994).

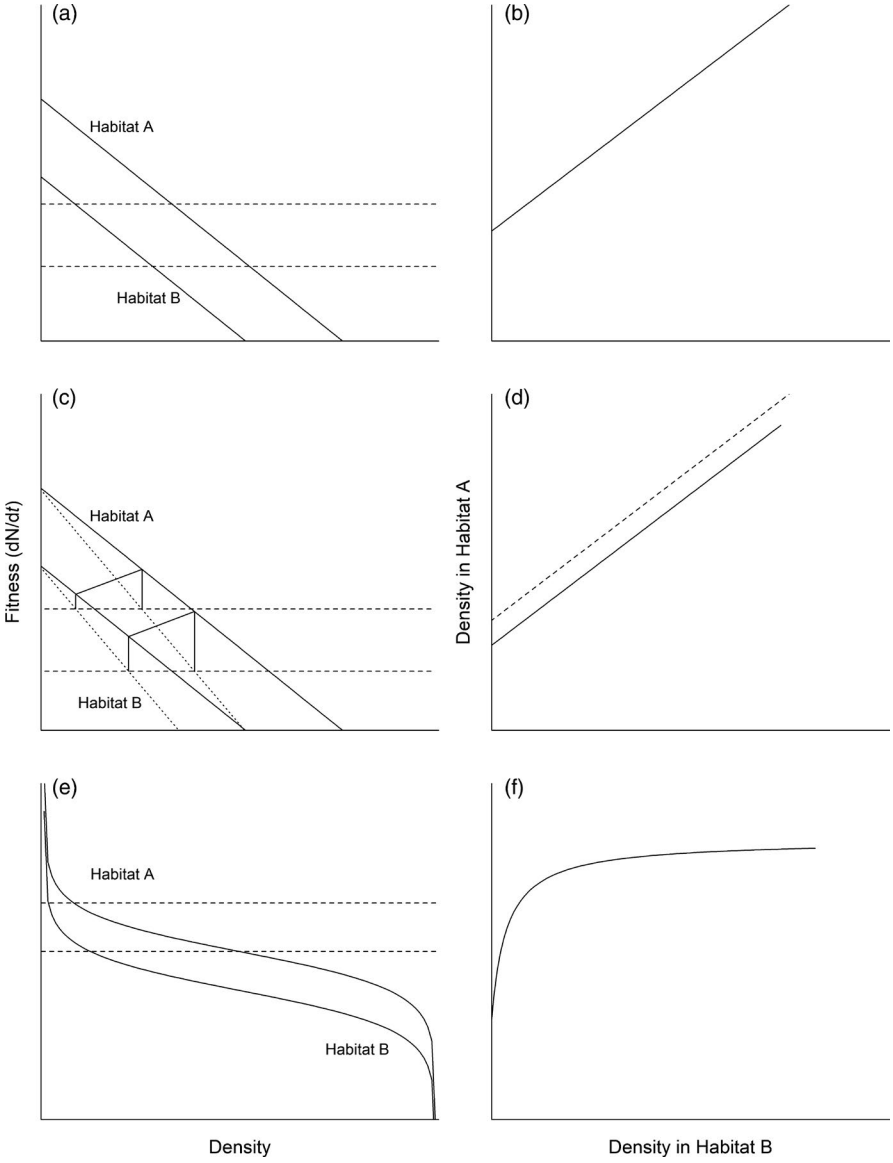

FIGURE 1 Theoretical fitness–density relationships and resulting isodars under the ideal-free distribution (IFD; a, b), the ideal-despotic distribution (IDD; c, d) and the ideal-preemptive distribution (IPD; e, f). In panel a, fitness declines as a function of density in two habitats of differing quality (solid lines, where habitat A is superior). The horizontal lines connect the densities at which fitness is equal in the two habitats. The pair of densities at these intersections produce the isodar in panel b; in this example, the inferior habitat (B) is not selected until habitat A reaches a certain density (density-dependent habitat selection). In panel c, the solid lines represent the quality of the habitats (similar to panel a), but territorial interference by dominant individuals causes reduced perceived fitness, altering the individual's habitat selection (dashed lines). The adjustment to fitness caused by territorial interference is demonstrated by connecting the true with perceived habitat quality (vertical lines). If individuals' perception of habitat is influenced by dominants (e.g. dashed horizontal lines indicating the habitat choice), they might select habitat of lower quality than they would otherwise, and fitness between habitat classes would no longer be equal. Panel e corresponds to fitness–density curves associated with differing site quality, where individuals preemptively select the best available site (Falcy, 2015; Morris, 1994). Figures adapted from Morris (1994)

Evaluating density-dependent habitat selection using an isodar approach has utility beyond simply distinguishing between ideal-free and ideal-dominant theoretical distributions. For example, an isodar intercept different than zero, as in Figure 1b, can reveal differences in resource availability between habitats (quantitative differences), while a slope significantly different than 1 suggests differences in habitat structure (qualitative differences; Morris, 1988, 1994, 2003a). These findings would have important conservation implications for many species, as they can indicate that a population is likely to achieve greater densities or increase more rapidly in one habitat type than another. In contrast, an intercept of zero, coupled with a slope of 1 indicates no apparent difference between habitat types (Morris, 1988). Testing theoretical habitat selection distributions can further reveal fundamental differences in how density-dependent habitat selection operates within a population (Rodenhouse, Sherry, & Holmes, 1997). An IDD or IPD, for example, can demonstrate the potential for mismatches between the realized and fundamental ecological niche, and may imply source–sink habitat dynamics (Pulliam, 1988, 2000). Under these circumstances, intraspecific competition and territoriality may have a strong influence on habitat selection processes (Pulliam, 1988; Pulliam & Danielson, 1991), and species' presence or density may not be tightly correlated with components of fitness such as reproductive success or survival (Uboni, Smith, Stahler, & Vucetich, 2017; Van Horne, 1983). Predictions of habitat suitability based on IFD are inappropriate in this case, and may lead to false conclusions (Mosser et al., 2009; Van Horne, 1983). Evidence of density-dependent habitat selection from an IPD or IDD also has strong implications based on predictions of a source–sink structured population (Morris, 2003a; Mosser et al., 2009; Pulliam, 1988). Territorial space-use distributions specifically suggest disproportionate individual contributions to population growth, leading to reduced effective population size (Falcy, 2015; Haché et al., 2013). Such considerations become increasingly relevant in the context of endangered species conservation, recolonization

or reintroduction of large carnivore species and translocation projects.

Here, we explore competing hypotheses about the habitat selection of a large, territorial, predator of conservation concern (grey wolves *Canis lupus*) by comparing observations of density-dependent habitat selection to that predicted by the IFD, IDD or IPD. To accomplish this, we applied isodar analysis to a 20-year time series of observational data gathered during a period of recolonization to the Upper Peninsula (UP) of Michigan, USA. Because of territorial behaviour at the pack level, we expected wolf isodars and fitness–density relationships to be more consistent with IDD (Figure 1c,d) or IPD (Figure 1e,f) than with IFD (Figure 1a,b). However, territorial species might behave according to an IFD if new arrivals or dispersing individuals respond to cues about density from existing occupants and use alternative sites rather than challenge existing competitors (Fretwell & Lucas, 1969). This scenario is plausible because wolves advertise their presence vocally as well as by intensively scent-marking territory boundaries (Mech & Boitani, 2010). Direct competition may be uncommon at relatively low densities because if some habitat sites are unoccupied, the risk of challenging current occupants might outweigh the cost of finding an alternative site, even if the alternative site is of slightly lower quality (e.g. Cassidy et al., 2015; Cubaynes et al., 2014). Although wolves' recolonization behaviour has been broadly studied, the role of density-dependent habitat selection and its implications for restored and expanding populations have not been previously addressed.

2 | MATERIALS AND METHODS

2.1 | Overview

We implemented isodar analysis by observing how wolf density covaried spatially across three different classifications of habitat during the 20-year study period. We generated spatially varying estimates of density from observations of pack size and location using aerial radiotelemetry and ground track surveys, coupled with Bayesian state-space models to accommodate uncertainty in observed pack counts and estimates of territory size (Figure 2). Differences in habitat were identified by evaluating landscape features (e.g. prey density, human density, land cover type) with principal components analysis (PCA). We used PCA results in conjunction with a GLMM of wolf occurrence to establish the most important predictors of wolf habitat and used them as a basis for isodar analyses. For each isodar analysis, locations on the landscape were classified as belonging to either high- or low-quality habitat classes (habitat A vs. habitat B, per Figure 1). The three pairs of classifications represented low and high prey availability, low and high risk of human conflict and low and high preferred land cover classes (Figure 2) as demonstrated in Section 2.5. We evaluated isodars with respect to each habitat type independently, while also incorporating interactions between habitat types.

2.2 | Study system and data collection

We conducted our study in the UP of Michigan during 1994–2013, a time period when wolves were recolonizing. Wolves primarily prey on white-tailed deer *Odocoileus virginianus* in this region, particularly in winter (DelGiudice, McCaffery, Beyer, & Nelson, 2009; Vucetich et al., 2012), though seasonal variation in diet is known to exist (e.g. Gable et al., 2018). Deer abundance is often constrained by long winters with heavy snowfall (Potvin et al., 2005). Many deer in the UP are partially migratory, especially at times and places when snow depth exceeds ~30 cm, leading to spatial variation in winter prey availability (O'Neil, 2017; Potvin et al., 2005; Witt, Webster, Froese, Drummer, & Vucetich, 2012). We live-captured wolves and fitted them with very high frequency radiocollars (Telonics, Inc., Mesa) during spring and summer each year (details in Appendix S1).

2.3 | Wolf pack sizes, territories and density estimation

To estimate wolf density each year within each grid-cell on the landscape, we first estimated the size and location of each pack using a combination of aerial radiotelemetry and ground tracking data. We quantified baseline pack territory boundaries using utilization distributions (UDs; Worton, 1989) when radiotelemetry data were available, and minimum convex polygons from ground tracking data otherwise. We then derived spatiotemporal variation in density from Bayesian state-space models of pack counts and territory size. This modelling framework provides a systematic approach for analysis in the presence of imperfect observation by accommodating uncertainty and missing data with respect to the pack count and territory observation processes (Kéry et al., 2009).

2.3.1 | Pack counts

We organized all pack observations into a data matrix with a row for each pack observed during the study period and a column for each year of the study. The elements of this matrix represented annual estimates of pack size, derived primarily from track surveys and supplemented by aerial telemetry (Appendix S2). Each winter all passable roads were travelled by truck or snowmobile while snow conditions were suitable for tracking (typically between December and March). Trackers recorded all sign, such as territory markings, scat and tracks. During the earlier portion of the study (1994–2006), track surveys were conducted in each of the 21 individual survey units that collectively represent the entire UP, and packs were assumed to be detected at least once via the track surveys on an annual basis (Appendix S2: Figure S1). As survey data accumulated, effort was increased in areas where packs had been previously detected to obtain accurate counts. Roads

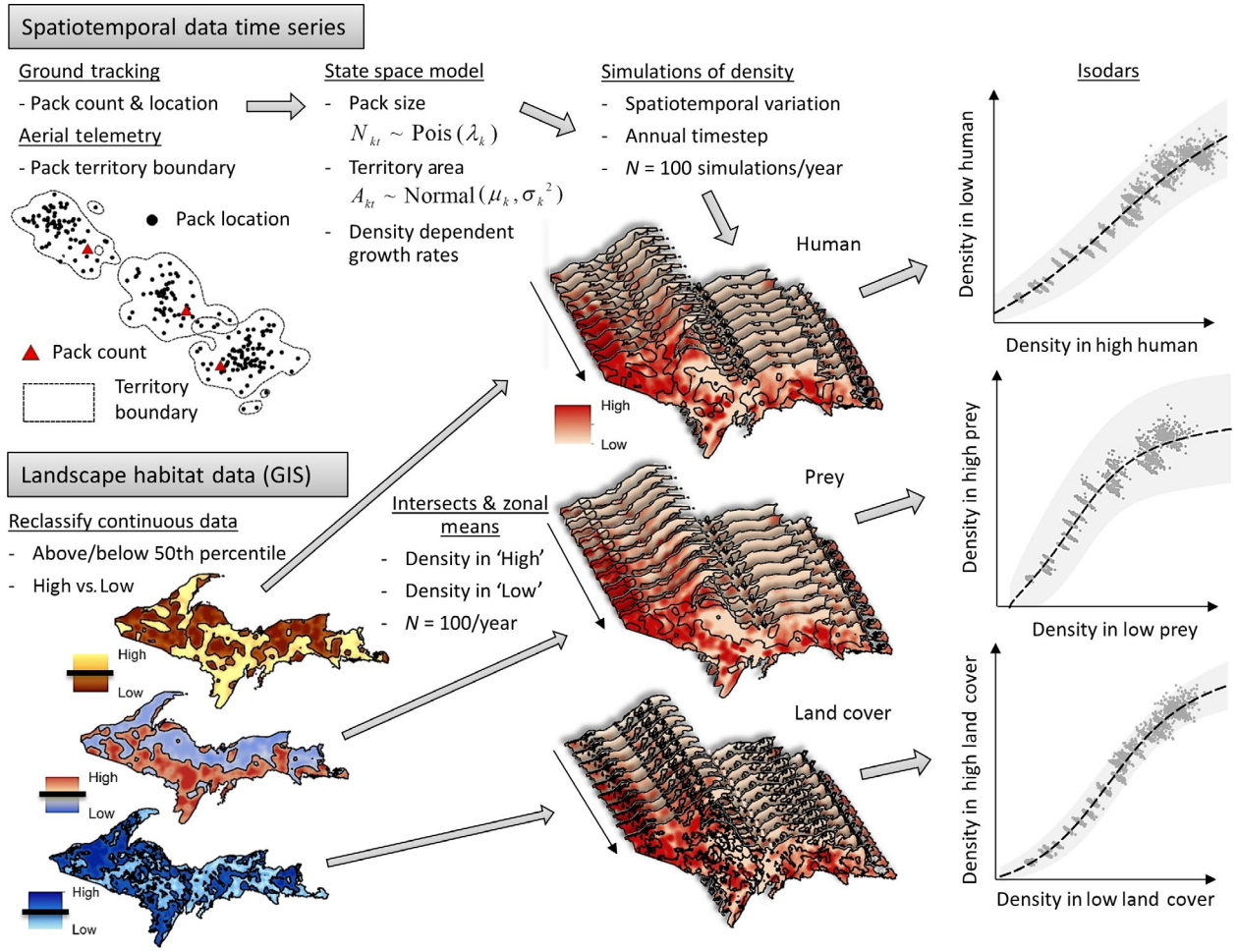

FIGURE 2 Diagram showing data and analytical steps taken to model spatiotemporal variation in wolf density and compare densities across time and among habitat characterizations using an isodar approach. In the first step, information on pack locations and size are combined on an annual time step from a combination of radiotelemetry and ground tracking data (annual census). Next, a state-space model was developed to incorporate uncertainty, missing data and imperfect observations of pack and territory sizes. Simulations were performed to generate multiple realizations of spatiotemporal wolf densities (100/year). Landscape attributes were informed by preliminary habitat analyses of continuous raster data indicating important predictors of wolf presence, and these were reclassified into discrete classes using values above and below the annual median value (high vs. low). Isodars were then simulated by calculating zonal means of wolf density within each discrete class for each habitat, and generating scatterplots of wolf density in these habitat classes across time (density-dependent habitat selection). The analysis was applied to grey wolves in the Upper Peninsula of Michigan, USA, 1994–2013

and trails were surveyed multiple times until accurate counts could be made (Appendix S2). An accuracy assessment of these methods was conducted during a separate 4-year study (2001–2005), where two independent wolf surveys were conducted simultaneously. The methods described here obtained similar counts as those from the more rigorous survey (described in Huntzinger, 2006; Vucetich et al., 2012), with an average difference of 4%. For the later portion of the study period (2007–2013) the survey units were visited according to a stratified sampling design (Potvin et al., 2005; Appendix S2: Table S1). Pack territories were assigned 'NA' within the corresponding matrix element during the years following the change in sampling design, allowing these values to be imputed by state-space models (Section 2.4). Population size derived from the winter track survey was assumed to be a minimum count (Potvin et al., 2005).

2.3.2 | Territory boundaries

To estimate the area, location and boundaries of each pack territory, we developed pack UDs using radiotelemetry data and supplemented those data with track survey data. We located radiocollared wolves by fixed-wing aircraft weekly. Territories were typically monitored by aerial telemetry relocations from at least one radiocollared wolf in each pack. Territories were also visited during the tracking survey, allowing approximate boundaries to be estimated when telemetry data were unavailable. We delineated territory boundaries each year using the following framework: If ≥30 telemetry locations were available for a pack during a year, we estimated its home range for that year, denoted *t*. If there were <30 locations for year *t*, but ≥30 locations were available over a 3-year time period ($t-1, t, t+1$), then we generated the pack's home range using locations from that 3-year period.

We used a fixed kernel density estimator to create a UD for each home range. The kernel bandwidth was estimated using the 'plug-in' method (Duong, 2007), after first removing outlying locations (≥5 km from territory; Fuller, 1989) and transient wolves (i.e. those that did not consistently occupy a territory). We defined the home range as the 95% volume isopleth from the UD. Home ranges and bandwidth estimators were analysed using packages ADEHABITATHR and KS in R 3.2.2 (Calenge, 2006; Duong, 2007; R Core Team, 2015).

For cases when fewer data were available, we generated long-term home ranges using a combination of telemetry locations and tracks from ground surveys. For example, if a home range had been generated for previous years, but the pack was only subsequently being monitored by track surveys, then we used the most recent telemetry-based home range. Otherwise, if we could not obtain ≥30 telemetry locations for a pack, we estimated its territory using a minimum convex polygon from all track survey locations across all years. Of all pack-year territory estimates (n = 1,616), 67% were created using telemetry data (>30 telemetry locations, n = 1,079). Due to inherent uncertainty in this approach, all subsequent territory boundaries were considered baseline estimates, with sizes and boundaries allowed to vary when making inference from state-space models.

2.4 | State-space models of wolf density

We implemented state-space models within a Bayesian analytical framework (Hostetler & Chandler, 2015; Kery & Schaub, 2011) to estimate wolf density across the study area while accounting for the knowledge that we could not obtain perfect observations of counts and territory sizes. The state-space model is a hierarchical model consisting of two sets of equations: one for the true, but unknown state (here, pack size), and the other to link the actual observations (pack counts) to the true process (Kery & Schaub, 2011; Royle & Dorazio, 2008). Denoting pack = k and annual timestep = t, our model for the true latent state was

$$N_{kt} = N_{kt-1} \exp(r_{kt} + b_k(\log(N_{kt-1})), \quad (1)$$

where r_{kt} represents pack-specific growth rate, while b_k is a parameter for density dependence (also estimated at the pack level). This model follows the discrete time parameterization of the Gompertz model (Hostetler & Chandler, 2015; Koons, Colchero, Hersey, & Gimenez, 2015), thus assuming population regulation at high relative densities. Following Koons et al. (2015), we re-specified this model on the logarithmic scale

$$\log(N_{kt}) = x_{kt} = x_{kt-1} + \alpha + \beta_k x_{kt} + \lambda_{kt}, \quad (2)$$

with β_k as the coefficient for b_k, and λ_{kt} for r_{kt} (growth rate on the log-scale). We added a term α to model an expected growth rate from low density (e.g. at population level; Koons et al., 2015); each pack's growth rate was allowed to vary from the overall population growth rate, with the strength of density dependence also varying by pack. Pack-specific offsets to the overall expected growth rate were assumed to be drawn from a normal distribution, $\lambda_{kt} \sim \text{Normal}(\bar{\lambda}_k, \sigma_k^2)$, with a mean annual growth rate $\bar{\lambda}_k$ and process variance σ_k^2 allowing for environmental stochasticity (Kéry & Schaub, 2011). The state-space model thus involved the process model $x_{kt} = f(x_{kt-1}) + \varepsilon_{kt}$, where $f(x_{kt-1})$ incorporates the right hand side of Equation 2 as well as the process variance error term, while the model for pack observations (y_{kt}) was $y_{kt} = g(x_{kt}) + \eta_{kt}$, with a Poisson error distribution specified following Koons et al. (2015). This equation relates the counts back to the unobserved process, while accounting for imperfect observation through the observation error term (Kéry & Schaub, 2011).

We assigned an uninformative normal prior distribution for initial pack size with truncation at 0. The prior distributions for λ_{kt} and σ_k were similarly uninformative ($\sigma_k \sim N(0, 10)$), thus allowing the process model to be informed primarily by the data. We placed constraints on pack size so that they could not exceed unrealistic estimates (specified as the maximum observed pack size across all years). We included additional information in our model to account for uncertainty in territory size, where territory area (denoted A, in km^2) was inferred from the best available information for pack locations. If telemetry data were adequate for a pack-year UD, then territory area was assigned a prior distribution specific to that pack: $A_{kt} \sim \text{Normal}(A_{kt}, \sigma^2_{A_k})$. Otherwise, the prior distribution depended on the pack's long-term average area: $A_{kt} \sim \text{Normal}(\bar{A}_k, \sigma^2_{A_k})$. If telemetry data were inadequate across all pack-years, then area was drawn from the distribution of all pack UDs informed by telemetry at the population level: $A_{kt} \sim \text{Normal}(\bar{A}, \sigma^2_A)$. Wolf density at the pack-year level was a derived parameter $D_{kt} = \frac{n_{kt}}{A_{kt}} \times 1{,}000$ (wolves × 1,000 km^{-2}).

We stored the full posterior distributions of all pack-year estimates from the state-space model for use in post-hoc analyses (see Section 2.5, below). We ran three Markov chain Monte Carlo chains, storing every 5th sample from 50,000 model iterations following a 20,000 iteration burn-in period. We used JAGS 4.2.0 (Plummer, 2003) within R 3.4.0 using JAGSUI (Kellner, 2015). We graphically compared the derived posterior pack size time series with observed pack counts to verify that the 95% credible intervals (CRI) overlapped the observed pack counts (Appendix S2: Figure S2).

2.5 | Isodar analysis

We used posterior distributions of pack-year densities combined with landscape habitat data to perform isodar analysis, using a stochastic simulation-based approach where we evaluated each isodar 100 times and drew our inference from the most probable outcomes. This was done to allow uncertainty with respect to pack-year counts, territory sizes and subsequent density to propagate through all proceeding analyses.

2.5.1 | Preliminary habitat analysis

Because isodar analysis requires comparisons of discrete habitat classes, we fit a preliminary GLMM to landscape habitat data as a

basis for identifying different habitat classes. We used a logit link function, with presence or absence of a pack as the binary response variable, and treated year as a random intercept. This model could be interpreted as a resource selection probability function estimating the overall influence of habitat predictors across the time period of study. The predictor variables in this GLMM were the principal component scores from three separate PCAs of correlated landscape predictors representing prey densities (buck harvest index and deer wintering complex habitat), human influences (road density, distance to highways, % impervious surface, % protected land) and landscape features (elevation, slope, forest-open edge, stream density). From this GLMM, we ranked habitat covariates by their effect size (*Z*-score) and delta score (predicted change in probability of selection corresponding to a unit change in predictor *x*). We selected the top three continuous predictors of habitat for subsequent analyses according to these rankings. Details about the preliminary habitat analysis are available in Appendix S3.

2.5.2 | Simulated isodars

We resampled from the posterior distributions of wolf density to construct 100 empirical isodars as follows: first, we drew a random sample from each pack-year posterior distribution of pack size, and a corresponding random sample from its posterior distribution of territory size. Next, we produced a new pack-year territory boundary based on the difference between the area of the baseline pack-year polygon and the new randomly sampled territory area. We assigned the sampled pack size estimate to the new pack polygon, and calculated wolf density at the pack territory level. After this was done for all pack polygons in the given study year, we combined all the new polygons and converted to raster format, ultimately generating 100 realizations of spatially varying wolf density for each study year. This resampling process was completed using Python 2.7.2 and the ArcPy module for ArcMap 10.4 (Environmental Systems Research Institute, Inc.) and supporting code and data are archived in the Digital Repository of the University of Minnesota (DRUM; https://doi.org/10.13020/0p2p-j920; Bump, O'Neil, Vucetich, Hoy, & Beyer Jr., 2020).

To classify habitat types using the continuous habitat predictors, we reclassified the relevant predictors into paired bins representing values above and below the median for each predictor (e.g. Falcy, 2015). We reclassified the three top-ranked predictors into 'low' and 'high' paired habitat classes based on the 0–49th and 51st–100th percentiles for each predictor, while discarding the median values. We recomputed the zonal mean wolf density within high quality (habitat A) and low quality (habitat B) with respect to each of the three habitat predictors (prey density, human influence and land cover). To investigate interactions between predictors, we performed a spatial intersection of the high- and low-quality classes for each pair of habitat predictors, and again computed zonal means within the intersected areas, thereby generating three additional isodars representing each pairwise interaction.

For each iteration within this process, we implemented isodar analysis using a scatterplot of the paired densities across the time series (*Y* axis = density in A, *X*-axis = density in B; see Figure 1b,d,f). We fitted linear, curvilinear and nonlinear models to each plot (Table 1), where the response variable (density in habitat A) represented the superior habitat based on the preliminary GLMM analysis. We used leave-one-out cross validation to evaluate each of the models based on root-mean squared error (RMSE), with lowest error indicating best fit to the paired densities (Stone, 1977). We stored the results of the best-fitting isodar models for each iteration. We reported the top model formulations for each isodar, corresponding to paired densities for each habitat predictor and each interaction between habitat predictors. The top model for each isodar was the model that most frequently ranked highest, from each of the 100 model fits. We plotted predictions based on the parameters and error estimates averaged across each top-ranked model.

2.6 | Wolf abundance estimation

We used the results of the state-space model to estimate overall wolf abundance and CRI for each year by summing the estimated number of wolves across all packs. Importantly, the application of the state-space model and the subsequent resampling of the posterior distributions allowed us to quantify uncertainty in overall

TABLE 1 Linear, curvilinear and nonlinear candidate regression models for fitting theoretical isodars to annual snapshots of wolf density occurring in separate habitat types. Candidate models include linear or curvilinear isodars representing ideal-free (IFD) or ideal-despotic (IDD) habitat distributions and nonlinear isodars representing ideal-preemptive distributions (IPD; Knight et al., 2008; Morris, 1994)

Model	Formula	Theoretical model (Morris, 1994)
Linear (M1)	$Y = \beta_0 + \beta_1 X + \varepsilon$	IFD/IDD; consumer-resource or additive interference
Log-Log (M2)	$\log(Y) = \beta_0 + \beta_1 \log(X) + \varepsilon$	IFD/IDD; continuous input or multiplicative interference
LogX (M3)	$Y = \beta_0 + \beta_1 \log(X) + \varepsilon$	IPD; fewer sites in higher quality habitat
Asymptotic (M4)	$Y = \phi_1 + (\phi_2 - \phi_1)\exp[-\exp(\phi_3)X]$	IPD; large differences in site quality between habitats
Logistic (M5)	$Y = \frac{\phi_1}{1+\exp[-(X-\phi_2)/\phi_3]} + \varepsilon$	IPD; unequal variances in site qualities between habitats

predicted abundance. We compared these overall abundance estimates with results of previous state estimates for the UP population to ensure that we had made reasonable assumptions about territory occupancy and pack sizes (Appendix S2: Figure S3; Michigan Department of Natural Resources, 2015). We provide a demonstration of the spatiotemporal variation in wolf density in the online Supplementary files (Video S1). All geoprocessing steps were completed in ArcMap 10.4 (Environmental Systems Research Institute, Inc.).

3 | RESULTS

3.1 | Pack counts, density and abundance

Wolf abundance in the UP increased from 80 to 658 during the study (U.S. Fish & Wildlife Service, 2017). The number of packs detected by track surveys and telemetry observations increased between 1995 (n = 32), and 2006 (n = 103), when the population census transitioned to a stratified sampling design (Appendix S2). In the following years, we estimated that a maximum of 137 individual pack territories (year = 2011) were present in the study area. Assuming that ≥2 wolves represented a pack, observations ranged from 2 to 18 wolves and increased over time, with annual mean counts per year ranging from 2.74 (SD = 0.86) to 5.14 (SD = 3.40). The average pack territory area estimated from telemetry was 283.10 km^2 (SD = 171.41), and 282.36 (SD = 158.33) using all data types (telemetry and track survey data).

Density-dependent state-space model estimates largely tracked observed data while incorporating additional uncertainty (e.g. estimating pack sizes when counts were unavailable), with annual average pack size estimates ranging from 2.52 (SD = 1.42) to 5.00 (SD = 2.78). Total abundance estimates from the state-space model were consistent with official estimates, with fitted point estimates of 83–657 and all 95% CRI overlapping official estimates for all years (Appendix S2: Figure S3). Population growth from low densities was strong across all packs ($\hat{\alpha}$ = 0.41 ± 0.04; mean ± SD). Density-dependent regulation was evident for 95% of

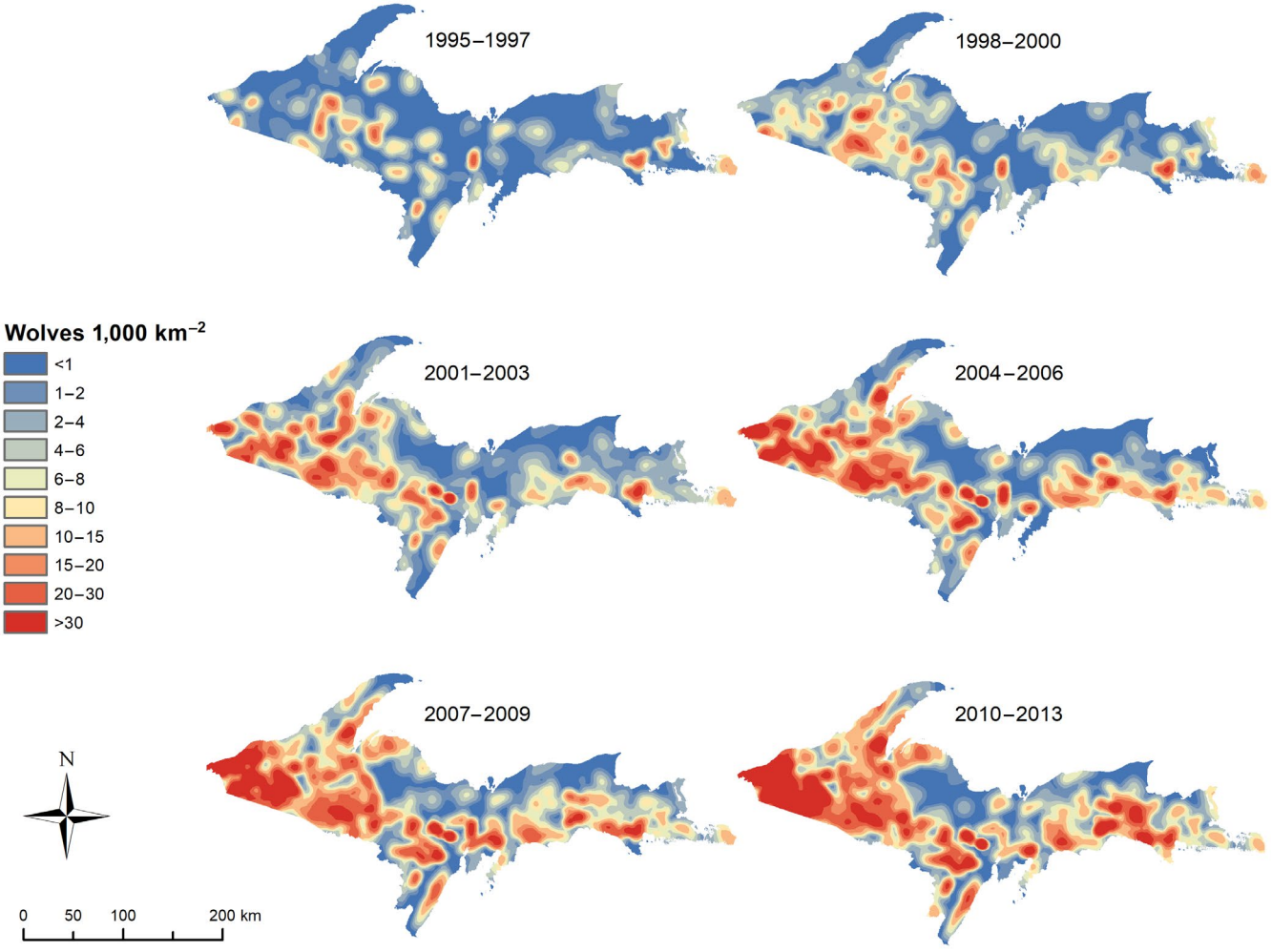

FIGURE 3 Time series showing spatiotemporal variation in wolf density. Annual estimates of wolf density at the pack level were derived from state-space models applied to radiotelemetry and tracking data. Initial territory boundaries were determined by utilization distributions from telemetry and tracking data, and post-hoc simulations were used to incorporate uncertainty in both territory size and pack counts. Estimates are presented as 3- or 4-year averages (e.g. 1995–1997 through 2010–2013)

packs (median $\hat{\beta}_k < 0$), and density dependence was predominantly negative across all packs ($\hat{\beta}$ = −0.28; 95% CRI = −1.05, 0.15). The population grew from 1995 to 2011 before apparently stabilizing (Appendix S2: Figure S3). Wolf density averaged across the study site was 1.97 wolves × 1,000 km^{-2} in 1995 and 14.41 × 1,000 km^{-2} in 2013. Density varied spatially and temporally, with greatest densities commonly occurring along the southwest border of the study area (>30 wolves × 1,000 km^{-2}; Figure 3; Video S1).

3.2 | Habitat categorization

The GLMM used to preliminarily categorize habitat types revealed that the top three predictors of wolf probability of territory selection were indices of prey availability (PC1-prey, $\hat{\beta} = 0.417, p < 0.001$), human influence (PC1-human, $\hat{\beta}$ = −0.244, $p < 0.001$) and land cover with high stream densities (PC2-land, $\hat{\beta}$ = 0.379, $p < 0.001$; Appendix S3: Table S1). Prey availability was represented by distance to and proportion of deer wintering complexes and annual buck kill reported from hunter surveys (PCA loadings reported in Appendix S3: Table S2). Human influence was represented by proportions of impervious surface, road density and the proportion of private versus public land (Appendix S3: Tables S2, S3). The principal component used for land cover was largely driven by stream densities, with greater stream densities associated with greater PC2-land values (Appendix S3: Tables S2, S3)

3.3 | Wolf density isodars

Wolf density differed between habitat types (Figure 4). More specifically, greater wolf density occurred with greater prey availability (PC1-prey; Figure 4a), lower human influence potential (PC1-human; Figure 4b) and greater stream density (PC2-land). By the end of the study, mean wolf densities exceeded 20 wolves × 1,000 km^{-2} where the land cover types favoured by wolves co-occurred (greater prey and stream densities, lower human influence; Figures 3, 4d–f). Isodars drawn from posterior distributions of wolf density within each pair of habitat classifications indicated that the relationships between wolf density in habitat A (superior habitat) and density in B (inferior

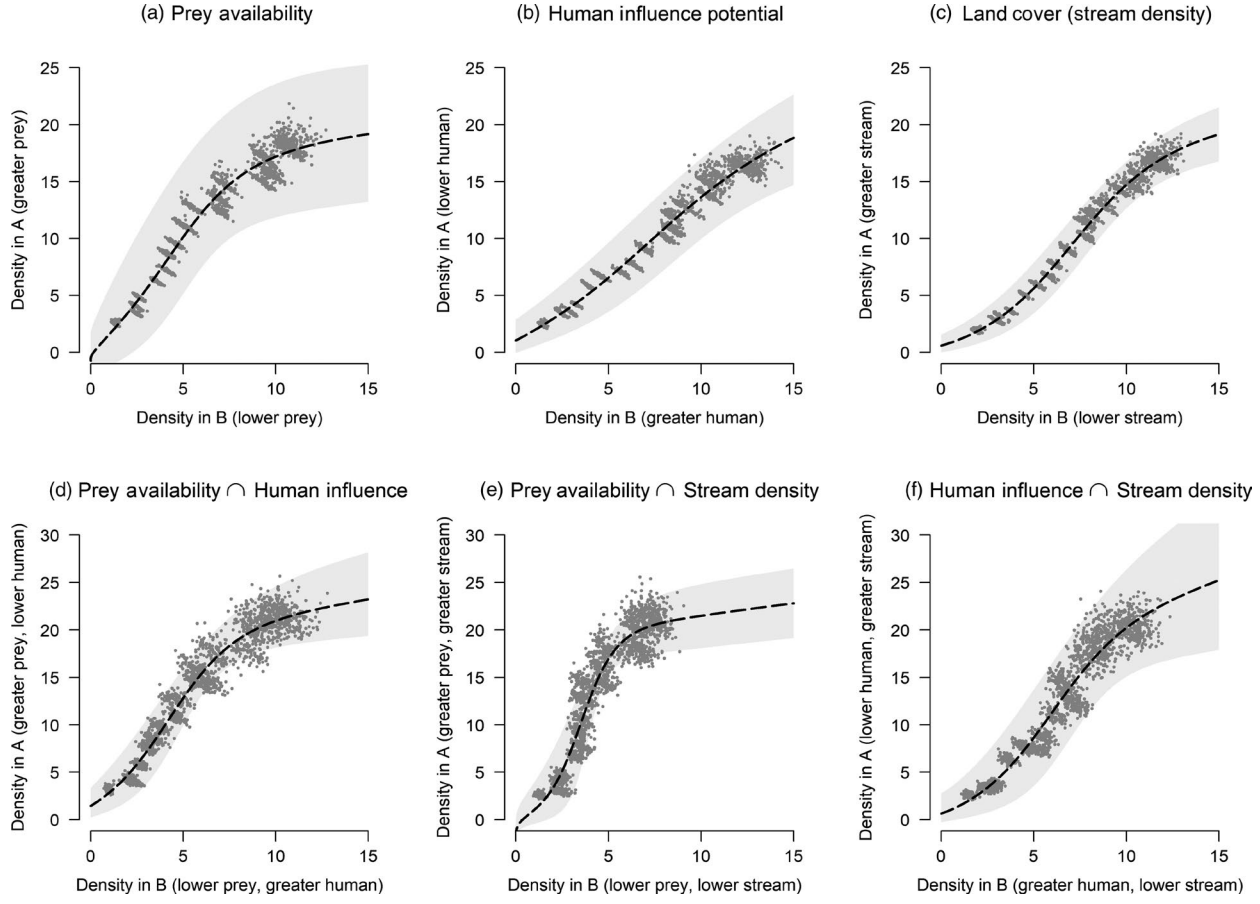

FIGURE 4 Empirical isodars of mean wolf densities occurring within contrasting habitat types representing low versus high human influence (a), prey availability (b), favorable land cover (driven by variation in stream density; c), and pairwise intersections between each different habitat category (d–f) in Upper Michigan, USA. Uncertainty in pack and territory sizes was incorporated into isodar analysis by plotting 100 realizations of the wolf density time series from posterior distributions of pack and territory size; posterior distributions were inferred from a hierarchical state-space model of wolf pack counts and territory sizes over the study's time series

habitat) were generally best fit by curved isodar functions; pairwise interactions between the different habitat classes also supported curved isodar fits (Table 2; Figure 4). Cross-validation statistics of the linear and nonlinear model fits are summarized in Table 2. Based on RMSE and visual examination of resulting isodar plots, the nonlinear isodars were most consistent with the IPD (Knight et al., 2008; Morris, 1994), indicating that wolves apparently used a preemptive site selection tactic while colonizing the study area. More precisely, each isodar was best characterized by a sigmoidal (S-shaped) nonlinear function; this shape was most evident when prey availability was intersected with land cover characterized by high stream densities (Table 2; Figure 4). Nonlinearity was least evident for the human influence isodar model, though the best fit was still the sigmoidal nonlinear model (Table 2; Figure 4).

TABLE 2 Cross-validation rankings for linear, curvilinear and nonlinear isodar regression models comparing wolf densities in habitats with high versus low prey availability, human influence and favourable land cover, as well as pairwise interactions between each habitat classification. M1 and M2 represent linear or curvilinear isodars, whereas M3, M4 and M5 indicate nonlinear regression model fits (see Morris, 1994). Nonlinear or curved isodars suggest preemptive density-dependent habitat selection (Knight et al., 2008; Morris, 1994). Regression models were fit to 100 realizations of the density time series via simulation from state-space model posterior distributions of wolf density within each respective habitat class; the top-ranked model is highlighted in bold for each isodar fit

	Model	*p*(best-ranked)	Mean RMSE
Habitat predictor			
Prey availability	M1	0.01	1.58
	M2	0.00	1.68
	M3	0.01	1.73
	M4	0.33	1.41
	M5	**0.65**	**1.35**
Human influence	M1	0.23	1.01
	M2	0.14	1.02
	M3	0.00	1.98
	M4	0.04	1.13
	M5	**0.59**	**0.98**
Land cover (stream density)	M1	0.08	0.9
	M2	0.06	0.95
	M3	0.00	1.94
	M4	0.01	1.19
	M5	**0.85**	**0.78**
Habitat interaction			
Prey availability × human influence	M1	0.03	2.15
	M2	0.12	2.13
	M3	0.00	2.68
	M4	0.02	2.06
	M5	**0.83**	**1.73**
Prey availability × land cover (stream density)	M1	0.07	2.91
	M2	0.00	3.42
	M3	0.03	3.12
	M4	0.01	3.30
	M5	**0.89**	**2.47**
Land cover (stream density) × human influence	M1	0.04	2.01
	M2	0.18	2.04
	M3	0.00	3.00
	M4	0.03	2.19
	M5	**0.75**	**1.88**

Abbreviation: RMSE, root-mean squared error.

4 | DISCUSSION

We found evidence that the mechanism underlying density-dependent habitat selection in wolves was most consistent with the IPD, indicating preemptive territorial selection of territories at the pack level. The primary indication of territorial habitat selection was evidence of a nonlinear isodar for all three categorizations of habitat considered in our analysis, as well as for interactions between those categorizations (prey availability, human influence and land cover types; Figure 4). We observed strong density-dependent habitat selection, especially with respect to measures of prey availability, stream densities and interactions between these habitat indicators (Figure 4a,c,e) where significantly greater densities were observed in habitat A than in habitat B across the time series. These results are noteworthy for several reasons.

Populations are commonly assumed to be at equilibrium with their environments (McLoughlin et al., 2010; Yackulic, Nichols, Reid, & Der, 2015), and habitat selection patterns are often presumed to follow the IFD (McLoughlin et al., 2010; Van Horne, 1983). However, territorial species are more likely to distribute themselves according to IDD or IPD theory, and our results suggested this to be the case for wolves recolonizing a portion of their historical range. Considering the specific life history of wolves (strong territoriality and intraspecific aggression; Cassidy et al., 2015; Cubaynes et al., 2014), we expected density-dependent habitat selection to occur in accordance with the IDD as opposed to the IFD. Instead, our analysis indicated that the IPD was the most appropriate theoretical model for our data. The IPD provides a reasonable theoretical framework for territorial density-dependent habitat selection in wolves, because it may be interpreted as a type of IDD and does not necessarily preclude dominant-subordinate behaviour (Haché et al., 2013; Pulliam & Danielson, 1991). Specific to wolves, preemptive site selection tactics and territorial cues such as howling and scent-marking could limit intraspecific conflict at low densities, thereby allowing the IFD or IPD to occur (Fretwell & Lucas, 1969). Moreover, territorial species do not always adhere to theoretical expectations and evidence from multiple studies suggests that underlying distributions can lie anywhere along a spectrum from IFD to IDD (Haché et al., 2013). We speculate that the IPD may be the most appropriate model during the colonization phase of a territorial animal, whereas the IDD may be more

likely when populations have reached an equilibrium (i.e. long-term growth rate ≈ 0) and density dependence has a stronger regulatory role. Although we could not confirm equilibrium in our study population, we suspect that suitable habitat was likely saturated by the end of the study (O'Neil, Beyer, & Bump, 2019). Distinguishing between theoretical models of density-dependent habitat selection, as we did with isodar analysis, is a valuable objective for any population because the underlying distribution has important implications for population dynamics (Falcy, 2015; Mosser et al., 2009).

4.1 | Conservation implications

Habitat selection patterns following IPD/IDD are likely for recolonizing large carnivore populations in North America and Europe (Carter & Linnell, 2016). Some implications of IPD/IDD include the potential for source–sink stuctured populations (Morris, 2003a; Pulliam & Danielson, 1991), and the application of predictive models to unoccupied potential habitats. First, source–sink population dynamics are generally not considered in management of wolves and other large carnivores, but are more likely to occur under IPD/IDD than IFD (Heinrichs, Lawler, & Schumaker, 2016; Mosser et al., 2009; Pulliam & Danielson, 1991). For example, it is thought that human offtake of wolves can reach 20%–30% of the population without causing population decline (Adams, Stephenson, Dale, Ahgook, & Demma, 2008; Fuller, Mech, & Cochrane, 2003; Gude et al., 2012; Murray et al., 2010). However, these conclusions are primarily based on findings that assume closed populations (Creel & Rotella, 2010) and do not explicitly account for source–sink structured populations. Our results imply that human-caused mortality could contribute to source–sink dynamics by altering the fitness consequences of density-dependent habitat selection. This scenario is most likely to arise when two major elements of habitat selection are prey abundance and the risk of human-caused mortality, a common circumstance for populations of large carnivores. In such cases, density-dependent mortality due to humans (Murray et al., 2010) and other factors would create an uneven landscape mosaic of fitness (O'Neil, Bump, & Beyer, 2017; Smith et al., 2010; Stenglein, Gilbert, Wydeven, & Deelen, 2015). If individuals respond to spatially varying mortality risk according to the IPD, the prediction would be that high-risk sites are selected only after low-risk sites have become occupied. Such an outcome could lead to high-risk sites acting as sinks where growth rate and density are suppressed by high rates of human-caused mortality, but populations are maintained by immigration from neighbouring sites (Adams et al., 2008; Stenglein, Gilbert, et al., 2015).

Our results confirm that prey availability and competition for prey, through preemptive occupation of high prey areas, are primary limiting factors in novel systems being recolonized by large carnivores. Further, assessment of isodars in occupied regions has utility for predicting densities in adjacent, unoccupied potential habitats. We demonstrated that an isodar approach can identify not only the attributes that influence population density, but also the strength and influence that density dependence has on habitat selection. For example, although we observed preemptive habitat selection patterns with respect to spatial variability in potential human impact, we also found that wolves appeared to exhibit stronger preemptive selection patterns with respect to increased prey availability, land cover with greater stream densities and interactions between these latter two habitat classifications. We suspect that stream densities were correlated with seasonal availability of alternative prey sources such as beavers (*Castor canadensis*; Gable & Windels, 2018; Metz, Smith, Vucetich, Stahler, & Peterson, 2012), while also implicating high quality hunting areas via travel corridors and increased prey encounter rates (Gable, Windels, Bruggink, & Homkes, 2016; Kauffman et al., 2007). For these reasons, we could hypothesize that large carnivore colonization to new areas can be predicted primarily by prey density or availability, provided limitations in prey availability can be detected. When limitations cannot be detected, which might be the case across large areas of potential habitat in the American west, large carnivore colonization may follow a pattern where human conflicts are the limiting factor (LaRue & Nielsen, 2008; Mladenoff, Sickley, Haight, & Wydeven, 1995), and future occupancy or density might be predicted solely by human densities or development. Existing patterns in density-dependent habitat selection can be useful tools for predicting future densities and potential expansion of large carnivore populations. These approaches can produce spatially explicit information about habitat availability, initial and expected densities and potential future population dynamics that would be relevant to future land management, designations of critical habitat and promoting awareness of potential human conflict.

4.2 | Analytical implications

We analysed isodars from continuous landscape data by building from methodology where habitat types are initially considered based on prior information or biological hypotheses (Figure 2; Falcy, 2015). Discrete habitat categories (A vs. B in the isodar) are then delineated using cutpoints representing statistical deviations away from the central value (Figure 2). Importantly, this approach facilitates the evaluation of multiple habitat components of the *n*-dimensional environmental niche via isodar analysis, presenting a unique opportunity to compare habitat preferences based on the strength of density-dependent habitat selection. We demonstrated how this can be done for individual habitat types, as well as for interactions between habitat types. This analytical approach, coupled with our findings of territorial and preemptive habitat selection by wolves, has intriguing potential when considering application to other study systems such as the Greater Yellowstone Ecosystem (GYE) of the western USA, where wolf and elk *Cervus elaphus* dynamics have been intensively studied since the reintroduction of wolves (Beschta & Ripple, 2016; Peterson, Vucetich, Bump, & Smith, 2014; Smith et al., 2010).

The role of density-dependent habitat selection has yet to be assessed as an element influencing space use by wolves and their cascading indirect effects in the GYE system (Peterson et al., 2014; Uboni, Smith, Mao, Stahler, & Vucetich, 2015; Uboni, Vucetich, Stahler, & Smith, 2015). Our findings imply that wolves

in Yellowstone may exhibit territorial and density-dependent habitat selection behaviour with respect to elk, a primary prey source throughout much of the region, especially the northern range. Elks are also likely to exhibit density-dependent habitat selection, but may conform to a more traditional IFD, where the intensity of use of secondary forage sources depends on the densities of elk using primary forage sources, as well as the availability of primary forage sources (a functional response in habitat selection; van Beest, McLoughlin, Mysterud, & Brook, 2016; van Beest et al., 2014). Importantly, density-dependent functional responses in habitat selection may contribute to observed changes and spatial patterns of browse intensity (e.g. trophic cascades) independently of predation pressure. However, density-dependent habitat selection by elk might also be influenced by wolves (Fortin et al., 2005; Kauffman et al., 2007; Kohl et al., 2018, but see Cusack et al., 2019). Evaluating density-dependent influences on habitat selection by wolves and elk in Yellowstone would be a key step toward further understanding the relative importance of wolves' influence on elk behaviour and selection patterns. If wolf densities influenced elk density-dependent habitat selection, it would then become possible to make predictions about where and when cascading effects on vegetation communities should most likely occur under varying scenarios of wolf density (e.g. importance of spatial heterogeneity; Peterson et al., 2014). We provide a novel analytical framework to explore these influences.

4.3 | Analytical limitations

To help guide future development of analyses building from long-term monitoring and census data, we acknowledge the challenges and limitations that we encountered when deriving spatiotemporal abundance information from broad, landscape-level data collection programs. First, although the effort and intensity of wolf monitoring in our study region was rigorous (Appendix S2; Potvin et al., 2005), we could not control for potential variability in detection rates of wolf territories and individual wolves (pack counts) across space and time. As a result, we acknowledge that annual estimates of territory presence and pack size were imperfect. To account for variation in detectability and improve estimates, a hierarchical modelling study design would be required, where pack size estimates would be modelled based on repeated counts or visits to verify site occupancy (Royle & Nichols, 2003; Royle, 2004). Unfortunately, such a study design would require replicate visits across a spatially representative sample of potentially occupied or unoccupied sites, likely increasing the cost and effort of surveys. We found that state-space modelling was a powerful alternative approach when annual repeated count data were unavailable, because it accommodates both observation and process error and produces a plausible range of estimates given the available data (Kéry & Schaub, 2011). Importantly, state-space models in a Bayesian framework can accommodate missing values and are often strengthened with prior information.

Second, we demonstrated evidence of IPD in recolonizing wolves based on the shapes of isodars fit to densities among three different characterizations of habitat. While curved isodars indicate territorial distributions (Falcy, 2015; Morris, 1994) and asymptotic or sigmoidal isodars suggest strong evidence of IPD (Morris, 1994), differences in measures of fitness between habitat classes could provide additional or alternative evidence of dominant or preemptive habitat selection (e.g. Mosser et al., 2009). According to the IFD, differences in habitat quality should manifest in differences in density among habitat classes while average fitness remains constant. In contrast, IPD or IDD should lead to differences in average fitness between habitat classes. Although we could not analyse metrics of fitness such as reproductive success in this study, analyses of adult survival within the same population indicated that survival varied spatially and was reduced in agricultural areas (O'Neil et al., 2017; Stenglein, Gilbert, et al., 2015). In addition, there were several observations of intraspecific killing in this population and adjacent populations (O'Neil, 2017; Stenglein et al., 2015), suggesting territorial interference. These findings, combined with the results of isodar analysis in this study, suggest that wolves distribute themselves and select habitat territorially. Furthermore, wolves appear to follow a preemptive habitat selection pattern during recolonization at the landscape scale, with growing potential for despotic behaviour (IDD) as localized densities increase, leading to competition for resources (Cassidy et al., 2015; Cubaynes et al., 2014).

5 | CONCLUSIONS

Evidence for preemptive habitat distributions is rare (Petty & Grossman, 2010; Sergio & Newton, 2003). Empirical evidence of a sigmoidal isodar can indicate complex fitness–density relationships across habitat gradients and reveal circumstances where predators may have strong impacts on local prey populations (detailed in Appendix S4). This scenario may be more common than generally appreciated, as large variance in territory or site quality is likely in habitats that are disturbed or fragmented. Our study documents non-linear isodars for a large carnivore species, implying an IPD that is generally considered to be a precondition for source–sink population dynamics (Morris, 2003b; Pulliam, 1988; Pulliam & Danielson, 1991). Source–sink dynamics are likely where species exhibit rapid growth and occupy interspersed habitats of contrasting quality (Heinrichs et al., 2016). These conditions occurred within our study system and are likely for large carnivores in other systems, such as areas in North America and Europe where many large predator species are currently recolonizing their historic ranges (Carter & Linnell, 2016). Understanding preemptive habitat selection and its potential to occur in a source–sink system is important for conserving species of concern such as wolves, because source habitats contribute disproportionately to population dynamics and are often difficult to identify (Heinrichs et al., 2016).

ACKNOWLEDGEMENTS

This research was funded by the Michigan Department of Natural Resources (MTU grant #751B430037 to J.K.B.). We are grateful for additional support from Federal Aid in the Wildlife Restoration Act

(Pittman-Robertson project W-147-R), National Science Foundation grants to J.K.B. (NSF ID#1545611, NSF ID#1556676), the DeVlieg Foundation and the Ecosystem Science Center (School of Forest Resources and Environmental Science at Michigan Technological University, MI, USA). The Michigan Involvement Committee of Safari Club International provided funding for radiocollars and other equipments. We thank Erin Largent, Robert Doepker, Steve Carson, Brian Roell and Chris Webster for assisting with data needs during analysis. Mike Haen, Brad Johnson, Donald Lonsway, Jeff Lukowski and Kristie Sitar assisted with capturing and radiocollaring wolves. Pilots Neil Harri, Dean Minett and Gordon Zuehlke collected collared wolf relocation data.

AUTHORS' CONTRIBUTIONS

S.T.O., J.K.B., J.A.V. and D.E.B. conceived the ideas and designed the methodology. S.T.O., J.K.B., J.A.V., D.E.B. and S.R.H. provided critical revision for important intellectual content. D.E.B. facilitated data collection. S.T.O. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data supporting this manuscript and code (R and Python scripts) used to analyse the data are archived for public use in the Digital Repository of the University of Minnesota (DRUM), accessible at https://doi.org/10.13020/0p2p-j920 (Bump, O'Neil, Vucetich, Hoy, Beyer Jr., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: O'Neil ST, Vucetich JA, Beyer Jr. DE, Hoy SR, Bump JK. Territoriality drives preemptive habitat selection in recovering wolves: Implications for carnivore conservation. *J Anim Ecol*. 2020;00:1–15. https://doi.org/10.1111/1365-2656.13199