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Spatial processes decouple management from objectives in a heterogeneous landscape: predator control as a case study

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Abstract. Predator control is often implemented with the intent of disrupting top-down regulation in sensitive prey populations. However, ambiguity surrounding the efficacy of predator management, as well as the strength of top-down effects of predators in general, is often exacerbated by the spatially implicit analytical approaches used in assessing data with explicit spatial structure. Here, we highlight the importance of considering spatial context in the case of a predator control study in south-central Utah. We assessed the spatial match between aerial removal risk in coyotes (*Canis latrans*) and mule deer (*Odocoileus hemionus*) resource selection during parturition using a spatially explicit, multi-level Bayesian model. With our model, we were able to evaluate spatial congruence between management action (i.e., coyote removal) and objective (i.e., parturient deer site selection) at two distinct scales: the level of the management unit and the individual coyote removal. In the case of the former, our results indicated substantial spatial heterogeneity in expected congruence between removal risk and parturient deer site selection across large areas, and is a reflection of logistical constraints acting on the management strategy and differences in space use between the two species. At the level of the individual removal, we demonstrated that the potential management benefits of a removed coyote were highly variable across all individuals removed and in many cases, spatially distinct from parturient deer resource selection. Our methods and results provide a means of evaluating where we might anticipate an impact of predator control, while emphasizing the need to weight individual removals based on spatial proximity to management objectives in any assessment of large-scale predator control. Although we highlight the importance of spatial context in assessments of predator control strategy, we believe our methods are readily generalizable in any management or large-scale experimental framework where spatial context is likely an important driver of outcomes.

Key words: Bayesian; *Canis*; *Canid*; carnivore; coyote; fawn; mule deer; neonate; *Odocoileus*; predator control; wildlife management.

INTRODUCTION

Under the guiding tenants of the North American Model of Wildlife Conservation (Organ et al. 2012), the lethal removal of problematic species is permissible for “legitimate purposes” following humane and scientifically sound strategies. Lethal predator control programs have been implemented to mitigate declines in threatened and endangered species (Harding et al. 2001, Smith et al. 2010) and to benefit economically valuable prey species throughout the United States, such as wild ungulates (Hurley et al. 2011, Kilgo et al. 2014) and livestock (Graham et al. 2005, Mabelle et al. 2015). In both cases, management is often conducted on the basis of assumed impacts of predation rather than from a mechanistic understanding of the interactions between predators and managed prey populations (Ballard et al. 2001, Harding et al. 2001, Brown and Conover 2011). Indeed, few studies have critically assessed predator control and those that have lack consistency in conclusions regarding

management outcomes (Salo et al. 2010, Hurley et al. 2011, Bradley et al. 2015).

The absence of consensus with regard to predator control is a manifestation of inconsistencies across studies, including differences in species’ life history, control strategy, scale of inference, and analytical methods (Graham et al. 2005). Many such studies are limited to correlating raw removal effort (e.g., absolute numbers of individual predators removed) with some metric capturing the desired management outcome (e.g., survival or population growth). Yet in doing so, researchers often omit relevant confounding factors that potentially mask or exaggerate the impact of predator control on management objectives. Such factors are often independent of predator control strategies and can include influential environmental variables, such as climatic state or phenology (Hunter et al. 2007, Griffin et al. 2011), that drive numerical responses in predator and prey populations or affect prey vulnerability (Hebblewhite 2005). Resource availability can also alter community composition (Tilman 1981), triggering additive or compensatory processes associated with species interactions within (Leo et al. 2015, Serrouya et al. 2015) and across trophic levels (Griffin et al. 2011). For

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example, the availability of alternative prey can sustain larger predator populations or modify consumption rates of managed prey, leading to variable impacts on managed prey populations (Knowlton et al. 1999, Hurley et al. 2011).

At a finer scale, the individuals being removed by control efforts are unlikely to have consistent impacts on prey populations (Jaeger et al. 2001, Blejwas et al. 2002, Swan et al. 2017). Behavioral differences between individuals attributable to experience, social status, and social learning are potentially important predictors of individual impact and the success of a given control program (Mitchell et al. 2004). Variation in spatial and temporal proximity to the desired objective (e.g., wintering yards, fawning sites) and proximity to management boundaries where recruitment of new individuals may be more frequent (Conner and Morris 2015, Lieury et al. 2015) are also likely to influence an individual's effect on management goals. Similarly, the size of a management area relative to the movement characteristics of the focal species can directly affect detection, risk, and rate of reestablishment following removals (Stoddart et al. 1989). Although individual variation in behavior is difficult to quantify, defining the spatial context of individual removals is frequently possible, yet to our knowledge rarely accounted for in these assessments (Conner et al. 2008).

Coyotes (*Canis latrans*) are often the focus of predator control efforts throughout much of North America, in part due to extensive range expansion over the last century that has increased conflict with humans for domestic livestock and wild game (Berger et al. 2008, Magle et al. 2014). A common method used to mitigate coyote–human conflicts in the western United States is aerial gunning (hereafter removal) from fixed-winged aircraft or helicopters (Brown and Conover 2011). The desired outcome of this strategy is the targeted removal of problem animals or broad reduction in predator abundance, followed by a decline in predator-induced additive mortality in prey populations (Wagner 1997).

Coyotes can be effective predators of neonatal deer fawns (*Odocoileus* spp.; Kilgo et al. 2014). In many areas of the western United States, aerial removal of coyotes is employed during winter in an effort to maximize coyote detection through snow tracking in remote and often difficult to access areas (Wagner 1997). This results in a temporal mismatch between the timing of removals in winter and the phenology of deer parturition in summer, when fawns are most vulnerable to coyote predation (i.e., within eight weeks post-parturition; Hall et al. 2016), and is a sufficient gap in time for immigration and replacement of coyotes to occur in some systems (Conner et al. 2008). However, timing of removals may negatively impact reproductive output in coyotes by disrupting pair formation and copulation (Gantz and Knowlton 2005), which in turn reduces the caloric demands of raising pups on surviving adults during the summer (Till and Knowlton 1983, Bromley and Gese 2001). Thus, winter removal strategy assumes a reduction in coyote abundance and/or number of reproductive packs, along with any associated effects like reduced predator-related additive mortality in fawns, persists through mule deer parturition several months later.

Although temporal mismatch is likely important, spatial context is almost always known. Here we demonstrate a conceptually intuitive approach to quantifying spatial match between management removals and objectives. We use data from a

predator control study in south-central Utah, USA to assess the spatial match between coyote aerial removal risk and mule deer (*O. hemionus*) resource selection during parturition using a spatially explicit, multi-level Bayesian model. Mule deer exhibit distinct resource selection patterns during parturition (Long et al. 2009, Freeman 2014), leading to spatial heterogeneity in the accessibility of fawns to coyote predation. Similarly, coyote removal risk is a product of encounter probabilities (i.e., probability of use by coyotes) and spatial constraints acting on removal crews (i.e., terrain). Thus, the efficacy of such strategy is dependent upon the degree to which removal risk overlaps mule deer habitat selection during parturition. As coyote and parturient deer space use, as well as aerial removal risk in coyotes, are inherently spatial processes linked to landscape features, we adopt a resource selection framework for each level within the hierarchical model (Johnson et al. 2006). Such an approach will improve our understanding of the impacts of predator management, while providing an objective method for evaluating the efficacy of specific proposed management strategies.

MATERIALS AND METHODS

Study area

We monitored aerial removal of coyotes, as well as space use by coyotes and mule deer, in a 1,200-km² area on Monroe Mountain, Fishlake National Forest, Utah (Appendix S1: Fig. S1). The study system is highly heterogeneous and characterized by a diverse array of elevation-dependent cover types that reflect differences in seasonal moisture regimes. The elevation ranges from 1,430 to 3,400 m with lower elevations dominated by shrub lands (*Artemisia* spp. and *Chrysothamnus* spp.), mid-elevations by pinyon (*Pinus edulis*), juniper (*Juniperus osteosperma*), gambel oak (*Quercus gambelii*), and mahogany (*Cercocarpus ledifolius* and *C. montanus*), and higher elevations by alpine meadows (*Achnatherum* spp.), sagebrush (*A. tridentata*), aspen (*Populus tremuloides*), and conifer (*Abies lasiocarpa*, *Pseudotsuga menziesii*, and *P. ponderosa*). Precipitation on Monroe Mountain occurs primarily in the form of snow from mid-to-late winter, with often highly variable spring mixed precipitation, late summer monsoonal rains, and dry falls.

Management

The USDA-Wildlife Services-Utah State Program (WS) actively implements a coyote aerial control program via helicopter and fixed-winged aircraft as a means of mitigating conflict with livestock and as part of an on-going statewide deer management plan to reduce coyote predation on mule deer fawns and to promote higher densities of harvestable deer (Utah Division of Wildlife Resources 2011, 2014). During the winters of 2012 through 2015, we capitalized on this existing plan by demarcating boundaries for WS flight teams with the purpose of overlapping removal efforts with concurrent, on-the-ground data collection related to coyote and mule deer demography (Appendix S1: Fig. S1). We imposed a before-after control-impact design (BACI) where removals were limited to one of two areas representing the northern and southern halves of Monroe Mountain (Appendix S1: Fig. S1). Removals were conducted on the northern site during the winters of 2012 and 2013, and the southern site during the winters of 2014 and

2015. The teams followed standard protocols, which aim to maximize removal efficacy within the logistical constraints of aerial removals (e.g., aircraft/personnel availability and weather). The frequency and timing of removal flights were dependent upon weather and usually occurred within 48 h of fresh snowfall, which facilitated coyote tracking by flight teams and is perceived to maximize efficiency of aerial removal efforts. Flight teams reported the locations of all animals removed using an on-board global positioning system (GPS).

Prior to each removal season, we live-captured coyotes and fitted individuals with GPS collars ($n = 16$; Lotek GPS 6000S, Isanti, MN, USA) using a combination of helicopter net-gunning, leg-hold traps, and cable restraints (USDA-NWRC IACUC: QA-1907, USU: IACUC-2182). We programmed GPS collar fix rates for 8-h intervals from September through May (non-summer) and 3-h intervals for

June through August (summer). We captured female mule deer using helicopter net-gunning and fitted individuals with GPS collars during the first week of March in 2012 and 2013 ($n = 21$; Advanced Telemetry Systems models G2110D and G2110E; Newmarket, Ontario, Canada) and again in March 2015 ($N = 57$; Advanced Telemetry Systems W300; BYU: IACUC-150110). We programmed collars to obtain locations at three (2013) or 11 h intervals (2015), year-round.

Model framework

We used a Bayesian hierarchical modeling framework to simultaneously evaluate coyote resource selection, coyote removal risk, and overlap with summer resource selection by deer (Fig. 1). Using a multi-level framework allowed us to account for parameter uncertainty within nested models. We

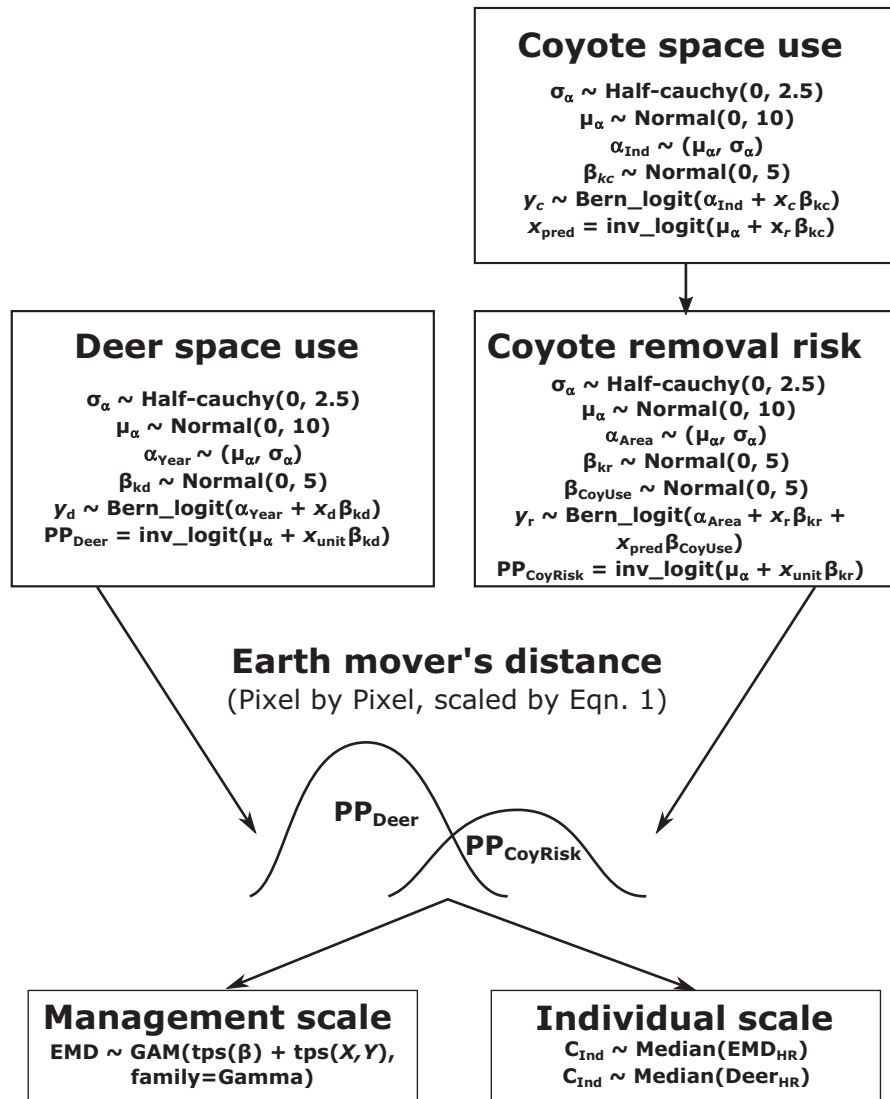


FIG. 1. Multi-level model specification for evaluating the spatial overlap between management actions and objectives. Each box corresponds to a dependent sub-model specification with prior distributions, hyperparameters, and model distributions ($y_{c,r,d}$). Subscripts of c, r, and d are for coyote, removal risk, and deer, respectively. α are the random intercepts (individual, year, or study area), X^* the covariates, and β^* the coefficients for each submodel. The subscript k^* is the number of parameters within a given model. Inv_logit transforms the linear function to a probability scale. HR are values estimated at the home range-level. TPS is a thin-plate spline used to estimate non-linearities in space using x-y coordinates. Arrows represent the hierarchical flow of sub-model output during simultaneous model fitting. x_{pred} are model-predicted data, x_{unit} are pixel-level covariates for the Monroe Mountain management unit, and PP are pixel-by-pixel model estimates.

built all models in R (v3.3.1; R Core Team 2016) using rstan (v2.11.1; Stan Development Team 2015; Appendix I).

Spatial data and sub-model specification

We incorporated a number of ecologically relevant spatial covariates in our sub-models (Appendix S1: Table S1), each of which was hypothesized to influence species-specific resource selection or coyote vulnerability to aerial removal. We included distance to water and to tertiary roads (i.e., unpaved roads), but did not include primary and secondary roads (i.e., paved roads and highways) as these were limited to the margins of the study system and therefore confounded by elevation and edge effects. We simplified LANDFIRE (2012) landcover classes into aspen, other hardwood (e.g., *Quercus* spp. and *Cercocarpus* spp.), shrublands, grasslands, pinyon or juniper, other conifer, mixed hardwood and conifer, rocky/barren, and tree cover >50% (see Appendix S1: Table S1). Each cover class was then converted into a continuous, distance-based metric by estimating the distance from each pixel to the nearest pixel of a given cover class. We also incorporated two terrain ruggedness metrics: vector ruggedness (VRM; Sappington et al. 2007) and terrain ruggedness index (TRI; Riley et al. 1999). Each ruggedness metric and categorical aspect (i.e., north, east, south, west, and flat aspect) was derived from 30-m USGS digital elevation maps (DEM, Utah Mapping Portal, 2015)⁷. We measured summer maximum normalized difference vegetation index (NDVI) as an index of forage-quality potential at 500-m resolution (Stoner et al. 2016). We assessed all continuous metrics for problematic correlations using a combination of Pearson's R ($R < 0.70$; Menard 1995) and variance inflation (VIF <4) by means of the R package usdm (Naimi 2015). We standardized (i.e., centered by means and scaled by one standard deviation) all continuous metrics to improve model convergence. Finally, so as to limit our predictive inference to the range of values evaluated, data used for prediction were truncated by the minimum and maximums, as well as standardized by the original means and standard deviations, for each covariate used in model fitting.

We used a mixed-effect logistic model to assess coyote resource selection within home ranges (i.e., third-order selection; Johnson 1980) following a used-available design (Johnson et al. 2006). We chose a third-order scale for the purpose of estimating a proxy for the likelihood of encountering coyotes during removal efforts. Thus, we included all diurnal fixes from coyote location data from December through March, corresponding to when coyotes were at risk of aerial removal. We estimated winter home ranges for each individual using kernel density (KDE, 95% isopleth) with a plug-in bandwidth estimator in R (KernSmooth; Wand and Ripley 2013). We then compared used locations with points sampled systematically within each home range (i.e., available locations) at the minimum resolution of our landcover layer (30-m grid) following Benson (2013). The model included random effects of individual crossed with year, as well as fixed effects for terrain ruggedness (VRM) and aspect, as well as distance to roads, water, and landcover class.

We assessed coyote removal risk using mixed-effect logistic regression. In this case, the locations where removals

occurred were compared to areas where removals did not occur, with the latter represented by a systematic sample of each 30-m pixel within the WS removal boundaries. As aerial removal risk is likely influenced by coyote resource selection, a proxy for the relative probability of encounter by WS personnel, we simultaneously fit coyote resource selection with removal risk. Thus, we estimated the relative probability of coyote use from the marginalized (i.e., population-level) resource selection model during each Monte Carlo iteration for inclusion as a covariate in the removal risk sub-model. In addition to coyote probability of use, we included a random intercept for year and fixed effects for aspect (given its relationship with snow cover, and therefore tracking conditions, attributable to variable sun exposure throughout the winter), distance to tree cover >50%, and terrain ruggedness (TRI). We chose TRI, which retains information pertaining to slope that VRM does not (Sappington et al. 2007), as a parsimonious way of representing the effect of terrain on accessibility by aerial removal teams.

We evaluated deer space use at the second-order scale to reflect the seasonal, elevation-dependent migration typical of mule deer populations in much of the western United States (Merkle et al. 2016). We chose a second-order scale because we were interested in characterizing site selection, rather than usage within a site (i.e., third-order selection), while capturing the shift toward higher elevation by parturient mule deer. Although usage within a site is also important, the coarse 11-h fix interval for a majority of deer (73%) precluded our ability to do so rigorously, particularly when constrained to the brief period when deer fawn were most at risk of coyote predation. Thus, deer location data were constrained to periods representative of summer ranges (i.e., timing of parturition) and specifically to periods from fawn birth dates to eight weeks post-parturition (Hall et al. 2016), corresponding to approximately June through August. We retained data from only those females that were gravid at the time of capture, survived through the middle of the following summer, and were likely to have dependent fawns during the anticipated window for parturition. We confirmed females were with fawns either visually during summer of each year or classified as having dependent young based on site fidelity and movement patterns using the program rASF (Mahoney and Young 2016). Fawn birth dates were estimated by hoof growth (Sams et al. 1996) or when parturient deer began exhibiting highly localized movements as identified by rASF. We further truncated an individual's data to include only those locations collected between the estimated birth dates and eight weeks post-parturition. Using these locations, we generated individual home ranges by KDE with an h-ref bandwidth estimator in R package adehabitatHR (Calenge 2006). We used a different bandwidth estimator for deer than for coyotes due to differences in fix interval and movement distributions, with the intent to produce more connected home ranges with fewer patches for both species. We then systematically sampled (30-m grid) "used" points within 80% isopleths to reduce the influence of a number of infrequent yet apparently spurious locations generated by collars with longer fix intervals. We represented availability, or potential sites where deer could have established summer fawning home ranges, by sampling points systematically within a minimum convex polygon encompassing all deer points plus

⁷ <https://gis.utah.gov/>

a 5-km buffer. We then compared these parturient deer home ranges with population-level availability using mixed-effect logistic regression (i.e., second-order selection; Johnson 1980). We included a random effect of year, and fixed effects for distance to landcover, distance to roads, distance to water, maximum NDVI, ruggedness (VRM), and aspect. We chose VRM as a ruggedness metric for deer because it represents a measure of terrain variability independent of slope and is commonly used in studies of montane ungulates (Sappington et al. 2007). Although deer migrate along an elevation gradient within this system, we did not include elevation as a covariate due to strong correlation with distance-to-landcover metrics such as aspen and conifer ($R > 0.70$).

While our approach for sampling “available” spatial data represents a census of availability at our finest spatial resolution (30-m grid; Benson 2013), the increased computation time required within a Bayesian framework necessitated subsetting these data in most cases. Thus, we evaluated the influence of systematic subsamples (e.g., every two or more pixels) on our representation of availability within each sub-model (Northrup et al. 2013). We retained the smallest sample that was representative of the “census” or that produced manageable model fitting times, whichever was achieved first.

Model evaluation

We used leave-one-out cross validation (LOOCV) and LOO information criterion (LOOic) to assess absolute model fit (R package loo v0.1.6; Vehtari et al. 2017), which as approximations of out-of-sample cross validation and prediction helped to reduce the potential for model overfitting. We implemented model selection within each sub-model set independent of the overall multi-level model in an effort to simplify the selection process at later steps. All sub-model sets included a null fixed-effect model for comparison with more complex models, which provided a means of insuring covariates explained variations in the data in a meaningful way. We then incorporated the single best sub-models for deer and coyote resource selection in the overall model and interpreted variable significance by posterior credible interval overlap with zero. In all cases, we confirmed proper model convergence with R -hat estimates < 1.1 , Monte Carlo errors at least one order of magnitude smaller than mean estimates, and through trace diagnostics for all model parameters. In addition, we confirmed all Pareto shape parameters (k) were < 0.5 to ensure unbiased approximations of LOO (Vehtari et al. 2017). Finally, as an additional qualitative measure of model fit, we performed posterior predictive checks for the final model by plotting observed against model-predicted values (Gelman et al. 1996).

Model synthesis

To address the question of scale in predator control, we generated posterior predictions for the probability of coyote removal and summer deer use for each 30-m pixel across the management unit (UDWR Monroe, Unit 23). We estimated congruence (i.e., overlap) between posteriors for removal risk and deer probability of use using the Earth Mover’s Distance (D_{EM}) in R package emdist (Urbanek and Rubner 2012), and weighted congruence to favor locations with a high median probability of use by deer (P_{Deer}) using Eq. 1

$$C = \frac{P_{Deer}^2 \times D_{EM}^2}{P_{Deer} \times D_{EM}} \times 1,000. \quad (1)$$

At the level of the management unit, we performed a post-hoc assessment using generalized additive models (GAMs) with Gamma errors to evaluate the influence of elevation, ruggedness, and distance to tree cover on weighted congruence metric, while accounting for spatial autocorrelation with isotropic thin-plate smooths (R package mgcv; Wood 2011). At the level of the individual, in cases where collared animals were removed, we estimated the median and coefficient of variation (CV) in probability of use by deer across all 30-m cells within a coyote’s home range. For those removals lacking home range data, we generated biologically meaningful buffers around removals by simulating movement trajectories, and therefore home ranges (1,000 minimum convex polygons per removal; Moorcroft et al. 2006, Van Moorter et al. 2009), using a hidden Markov model fitted to the complete coyote GPS data set (R package moveHMM; Michelot et al. 2016). We then used these simulated home ranges to derive a posterior expectation of median probability of use by deer for each individual, which in turn can be interpreted as the degree to which that individual overlapped mule deer parturition habitat and the potential contribution of that individual toward mule deer management objectives.

RESULTS

Coyote resource selection

We used GPS data from 11 coyotes (fix success: $\mu = 94.1\%$, $\sigma = 3.5\%$) with sufficient location information during the winter at risk period, resulting in 16 seasonal home ranges from nine different packs. We evaluated 26 models for coyote resource selection, including a single null fixed effects model (Appendix S1: Table S2). We originally included random effects for both individual and year given the sampling structure within our data. However, a sizeable number of pointwise Pareto k estimates were > 0.7 for all models including year, indicating potential bias in LOO estimates. Further inspection indicated problems with estimating the effect for the last year of the study. Thus, following the recommendations of Vehtari et al. (2017), we simplified our model structure by removing year as a random effect, which in turn dropped all Pareto k estimates below the acceptable threshold of 0.5. Furthermore, removing year from the model did not change the interpretation of fixed coefficients in any biologically meaningful way.

We did not consider coyote resource selection models with aspen due to problematic correlations with distance to conifer and mixed conifer/hardwood. Here, we derived inference from the most parsimonious top model (Table 1, Fig. 2a), which was also our best model based on LOOic (Appendix S1: Table S2). During daylight hours in the winter, coyotes selected for shrublands, rocky/barren cover, and water, as well as intermediate distances to grasslands and tertiary roads. They also selected rugged terrain, and east- and south-facing aspects (relative to north aspects). Coyotes avoided conifer, mixed conifer/hardwood, and non-aspen hardwood stands.

TABLE 1. Coefficient estimates for the coyote resource selection, coyote removal risk, and deer resource selection models.

Fixed effects	Coyote resource selection (third order)				Coyote removal risk				Deer resource selection (second order)			
	Mean	SD	Lower CI	Upper CI	Mean	SD	Lower CI	Upper CI	Mean	SD	Lower CI	Upper CI
Aspen									−0.102	0.028	−0.156	−0.047
Aspen ²									−0.054	0.020	−0.094	−0.014
Barren	−0.052	0.024	−0.096	−0.004								
Conifer	0.181	0.036	0.110	0.252					−0.560	0.033	−0.625	−0.496
Grass	−0.080	0.039	−0.157	−0.004					0.471	0.017	0.439	0.504
Grass ²	0.072	0.021	0.032	0.111					−0.130	0.009	−0.148	−0.114
Hardwood (other)	0.177	0.032	0.113	0.240					−0.360	0.020	−0.401	−0.320
Hardwood ²	−0.050	0.014	−0.078	−0.024					−0.078	0.016	−0.110	−0.047
Mixed forest	0.059	0.050	−0.039	0.159								
Pinyon/Juniper									0.730	0.025	0.680	0.779
Pinyon/Juniper ²									−0.262	0.009	−0.279	−0.244
Shrub	−0.106	0.025	−0.156	−0.057					−0.050	0.018	−0.084	−0.014
Shrub ²									−0.013	0.005	−0.023	−0.003
Tree Cover (>50%)					−0.036	0.121	−0.281	0.195				
Tree Cover ² (>50%)					−0.402	0.124	−0.664	−0.179				
Tertiary roads	0.068	0.031	0.008	0.129					−0.258	0.014	−0.286	−0.230
Tertiary roads ²	−0.062	0.015	−0.092	−0.032					0.043	0.004	0.035	0.051
Water	−0.118	0.023	−0.163	−0.075					0.575	0.015	0.545	0.604
Water ²									−0.270	0.013	−0.297	−0.244
Max NDVI									1.056	0.026	1.005	1.108
Max NDVI ²									−1.099	0.021	−1.140	−1.058
Ruggedness, TRI					0.461	0.139	0.180	0.734				
Ruggedness, TRI ²					−0.216	0.077	−0.368	−0.070				
Ruggedness, VRM	0.063	0.020	0.024	0.103					0.078	0.012	0.054	0.102
Ruggedness, VRM ²									−0.035	0.011	−0.056	−0.014
Probability of use by coyotes					1.436	1.938	−2.044	5.567				
East†	0.195	0.058	0.078	0.306	0.145	0.204	−0.267	0.535	0.357	0.027	0.305	0.409
South†	0.247	0.060	0.130	0.363	0.126	0.229	−0.336	0.559	0.056	0.030	−0.002	0.115
West†	−0.277	0.058	−0.392	−0.165					−0.377	0.028	−0.432	−0.323
No aspect†	0.260	0.456	−0.708	1.074					−0.451	0.102	−0.653	−0.258

Notes: Lower and upper CI are the lower and upper 95% credible intervals. PJ represents pinyon, juniper cover, VRM the vector ruggedness metric, and TRI the terrain ruggedness index.

†Reference groups are north aspect for deer and coyote resource selection and north, west, and no aspect for removal risk.

Coyote removal risk

A total of 182 coyotes were removed from the study site over 4 yr. We received removal locations for 156 and visited 106. The remaining 50 removal sites were either inaccessible due to winter conditions, had been covered by subsequent snowfalls, or sufficient time had transpired permitting scavengers to disperse the carcasses. The accuracy of aerial fixes was consistently within 50 m, indicating that the GPS error was usually less than our minimum spatial data resolution. We evaluated seven models for coyote removal risk and derived inference from the single best model (Table 1, Fig. 2b, Appendix S1: Table S3). In general, aspect did not influence coyote removal risk. However, coyotes were most susceptible at intermediate distances to tree cover. In addition, coyotes were much more likely to be removed in flatter terrain (Appendix S1: Fig. S2). The nonlinearity for ruggedness (i.e., TRI) indicated that the probability of coyote removal declined exponentially with increases in ruggedness. While not significant, the large, positive effect of coyote probability of use indicated that managers were removing

animals from primarily areas where encounter probabilities were high, namely open, flat terrain.

Deer resource selection

We had sufficient location data from 39 adult female deer with confirmed or probable dependent young from 2012 through 2015, resulting in a total of 51 summer home range estimates. Of these 51 probable fawning events, we confirmed six visually and estimated 45 using program rASF. However, rASF was less precise for some individuals with the longer fix interval collars deployed in 2015 (i.e., 2- to 7-d window). Thus, when fawning was confirmed as likely, we used the first day of the estimated parturition interval as the birth date for truncating location data. Eleven of these females (14 home ranges) summered on neighboring ranges outside the Monroe Mountain management unit. However, these ranges are also districts in Fishlake National Forest and consisted of a similar mosaic of landcover types and plant assemblages. Thus, the added power provided by these additional individuals increased the representative nature of

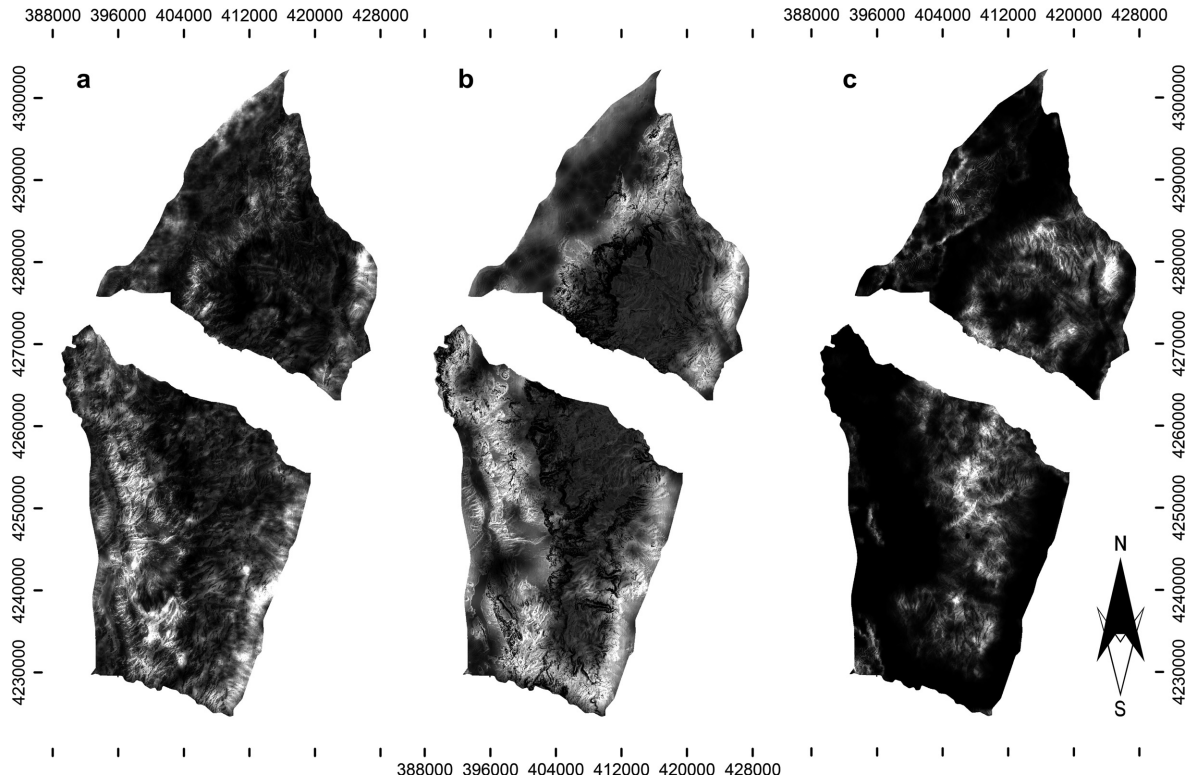


FIG. 2. Heat maps for the model predicted relative probabilities of (a) coyote use, (b) coyote removal risk, and (c) deer use on Monroe Mountain in Fishlake National Forest, UT. Dark to light is low to high probability, respectively. The x-y coordinates are in Universal Transverse Mercator (UTM Zone 12N, datum NAD83).

deer site selection during parturition for the region. Our sample of availability encompassed all lands that were potentially accessible to study animals, including these neighboring ranges, for the deer selection models only.

We evaluated 23 models for deer resource selection (Appendix S1: Table S4). LOOic strongly supported our top model for adult deer resource selection during the eight weeks post-parturition (Fig. 2c), indicating significant nonlinearities in all of our continuous metrics with the exception of distance to conifer (Table 1). The top model indicated that deer selected fawning sites near tertiary roads, shrublands, aspen, conifer, or hardwood, as well as intermediate levels of ruggedness (VRM) and NDVI. Deer avoided grasslands, pinyon-juniper, and water when selecting fawning sites. In addition, deer selected for home ranges on east-, south-, and north-facing aspects over west-facing and no aspect.

Congruence at the level of the management unit

All three sub-models exhibited good posterior predictive accuracy (Appendix S1: Fig. S2). The study-area median congruence between coyote removal risk and deer fawn site selection, after weighting by mule deer probability of use, was 0.25 (CV = 120.51) (Fig. 3). The GAM indicated substantial spatial variation in weighted congruence between removal risk and probability of use by deer (spatial smooths with $\text{edf} = 1,446.06$, Appendix S1: Fig. S3a). We tested models with elevation, ruggedness (TRI), and elevation with ruggedness. Model selection retained elevation ($\text{edf} = 37.97$) and ruggedness ($\text{edf} = 39.83$). However, the effect of elevation

was not likely to be biologically meaningful given the relatively flat relationship (Appendix S1: Fig S3c). Yet, congruence declined precipitously and nonlinearly as ruggedness increased (Appendix S1: Fig S3b).

Congruence at the level of the individual removal

The hidden Markov models performed well at simulating movement trajectories, and thus home ranges, when fitted using coyote GPS trajectories (Fig. 4a). Simulated home range sizes were larger than observed, but in general median home range size from simulations matched our observed sizes in cases where home ranges were known (Fig. 4b). In addition, median overlap with predicted relative probability of use by deer was also a close approximation for the observed values in known coyotes and in all cases were encompassed by the 95% highest posterior density interval (Fig. 4c, Appendix S1: Table S5).

DISCUSSION

Our primary objective was to evaluate the spatial match between spatially explicit removal risk in coyotes and space use by parturient deer. Our model, and the respective sub-models, accurately captured coyote (Arjo and Pletscher 2004) and deer resource selection (Long et al. 2009), as well as coyote removal risk, and exhibited strong predictive inference based on posterior predictive checks (Appendix S1: Fig. S2). Although intuitive, our results indicated that coyotes were generally most at risk of removal in areas with the

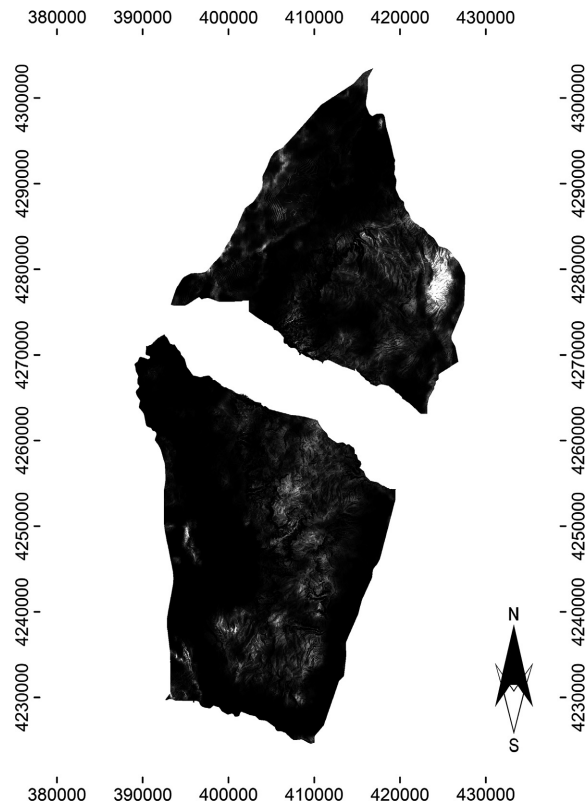


FIG. 3. Heat map of weighted congruence where lighter areas correspond to stronger congruency between coyote removal risk and deer resource selection in areas with higher probability of use by mule deer.

highest predicted (relative) probability of occurrence, which was represented by open shrublands in low-to-moderately rugged terrain during daylight hours in winter. However, after accounting for coyote resource selection, spatial constraints acting on the efficacy of removal indicated coyote removal risk declined as ruggedness increased or when near tree cover. Likely, flight crews were impeded by more rugged terrain due to safety concerns, requiring more attentive flying by the pilot and overall reduced detectability of coyotes. Although trees pose a similar safety concern, tree cover limits visibility and obstructs projectiles used in lethal removal, thereby providing refuge for coyotes. Our models also indicated a decline in removal risk at higher distances to tree cover, suggesting intermediate distances were most risky for coyotes. Intermediate distances are likely an artifact of WS targeting areas believed to be favored by mule deer (e.g., near tree cover) or due to differences in how coyotes respond behaviorally to aircraft, potentially affecting detectability as distance to cover increases (e.g., flight response vs. holding still when near and far from tree cover, respectively). There was no effect of aspect, at least relative to our expectations of coyote resource selection. This is not particularly surprising given the timing of flights to coincide with fresh snowfall (i.e., before south faces had an opportunity to melt off). Although we do not explicitly address how coyotes will respond to sustained aerial removals, we acknowledge that plasticity in coyote behavior may further mitigate the utility of such a management strategy as individuals learn to avoid aircraft, particularly in areas with ample tree cover favored by parturient deer (Freeman 2014). Nonetheless, our effort clearly highlights the spatial heterogeneity in coyote aerial

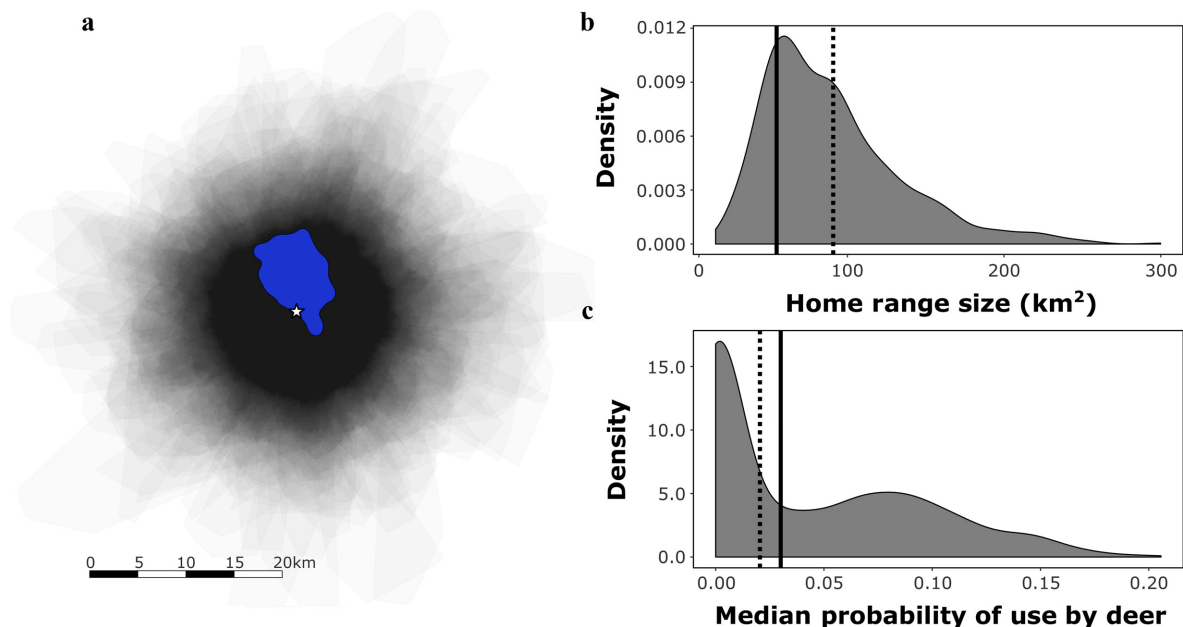


FIG. 4. (a) An example of 1,000 simulated home ranges for a removed coyote (white star) with a known home range (blue polygon). The darker shading corresponds to more frequent home range overlap in a given region of space. The densities for (b) 1,000 simulated home range areas and (c) median overlap with relative probability of use in deer, with observed estimates (solid line) and simulated estimates (dotted line).

removal risk and emphasizes the constraints acting on aerial removals as a management tool for mule deer (Knowlton and Windberg 1985).

We also evaluated the influence of elevation and ruggedness on the spatial congruency between management removals and parturient deer site selection. In this case, we found no effect of elevation and a strong negative, nonlinear effect of ruggedness on weighted congruency (Appendix S1: Fig. S3). Thus, not surprisingly, WS personnel are most effective at removing coyotes from areas favorable for deer when navigating less rugged terrain regardless of elevation (white colors in Figs. 2b, c, 3), but their success declines with increasing ruggedness likely as a consequence of operational challenges in mountainous terrain. However, declines in overlap are also indicative of differences in expectations of space use in both species, with coyotes generally preferring more open landcover classifications (e.g., barren ground and shrublands) relative to mule deer (e.g., forest; Table 1).

Predator control is often evaluated in terms of purely demographic processes. Yet, ignoring spatial structure may be critical and could either mask or exaggerate the perceived efficacy of control efforts. We highlight substantial spatial variation in the overlap between coyote removal risk and where deer fawns are likely to be encountered, and that the outcome of such management can be highly variable in heterogeneous landscapes at two distinct spatial scales. First, aerial control is potentially more impactful in areas where aerial risk is congruent with management objectives but likely to be inconsequential at broader management scales where overlap among focal species is low. Although this is intuitive, our approach provides an objective means of quantifying the potential of a given management tool when applied across broad landscapes, with the ability to distinguish favorable management units from other, more challenging units. Second, assessments of predator control have often assumed each management removal is equally impactful on the desired objective (e.g., Hurley et al. 2011). Yet, variation in the proximity of

removed predators to objectives (e.g., deer fawns, Fig. 5) will likely contribute to uncertainty regarding the outcome of predator control. Specifically, we anticipate ignoring spatial context will bias most evaluations of predator control programs (Stoddart et al. 1989). Here, for example, although the annual numbers of coyotes removed were consistent from year to year, removals during the winter of 2015 were predicted to be largely ineffective due to poor overlap with parturient deer site selection (Fig. 5). While detection and effort are likely key predictors of absolute removal risk, we could not explicitly account for these factors. However, our results are robust within the context of our primary objective in that we compare spatial congruence between removal risk and parturient deer resource selection. For example, increased removal effort will lead to a proportional increase in the relative probability of risk but will not change the spatial context of risk (i.e., low risk will remain low risk and vice versa). Our estimates of spatial congruence between removal risk and parturient deer resource selection should also be consistent regardless of effort, though the absolute measures of congruence will change. Similarly, we acknowledge that although animals were likely detected and pursued before ultimately being removed, initial encounter is a matter of detection. Documenting where an animal was removed with precision was more reflective of actual risk and therefore most relevant to our analytical goals. However, the hierarchical structure of the risk model helped to capture variation between years and across study areas that is likely attributable to variation in detection, density, and climatic conditions.

In addition to assessing match at the scale of a management unit, we provide a means of quantifying potential impact at the level of the individual removal by simulating home ranges (or biologically plausible spatial buffers) using fitted hidden Markov movement models. By intersecting these simulated home ranges with deer probability of use during parturition, we were able to derive a posterior expectation of overlap on a per removal basis. Doing so

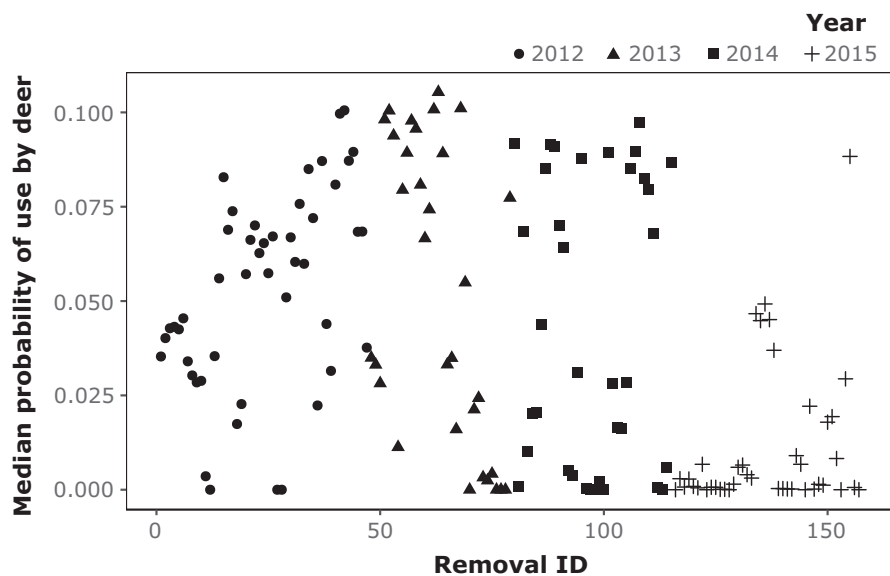


FIG. 5. The estimated median overlap with relative probability of use by deer for all 156 coyote removals. Larger median values indicate greater potential impact on mule populations.

clearly demonstrated the inequality among individual removals with regard to objectives (Fig. 5; Mitchell et al. 2004), suggesting the need to weight actions by their potential impact in a spatially explicit manner when evaluating the efficacy of a given management strategy.

We recognize that there are likely seasonal differences in coyote resource selection (Koehler and Hornocker 1991, Neale and Sacks 2001). By evaluating winter diurnal space use, we intended to address the issue of encounter probability during removal efforts, and therefore seasonal differences are likely of little consequence. We also recognize that our relatively small sample of coyotes may insufficiently represent coyote probability of use during the winter. However, a distinct advantage to a hierarchical Bayesian framework is that the uncertainty in probability of use is carried over to the removal risk model as a result of simultaneous model fitting. Thus, the uncertainty in probability of use and its role in removal risk is reflected in the credible intervals for this covariate (Table 1). With regard to simulating home ranges based on only winter removal locations, there is ample evidence to indicate that coyotes in the region are non-migratory and exhibit strong home range fidelity across seasons (Gantz and Knowlton 2005). In addition, we parameterized our hidden Markov models using the complete year-round location data sets, including both resident and transient individuals. Thus, our estimates of individual-level impact should be conservative. These estimates of overlap do not account for coyote resource selection within home ranges, which would accommodate shifts toward or away from areas within a home range utilized by parturient deer. Although we did not do so here because of limited spatial data from removed coyotes, the framework we have outlined could incorporate estimates of overlap weighted by probability of use estimates at finer than home range scales provided empirical data are available. Nonetheless, we feel confident that our estimates provide an effective measure for evaluating the variation in potential impacts of removed animals on deer management objectives.

Managers can use such spatial models to make objective decisions about where and when proposed aerial predator control should be employed, while reducing risks to human safety, unnecessary animal removals, and undue financial burden to wildlife programs. However, the ambiguity regarding management impacts is not reserved to predator control alone. The importance of spatial context in wildlife management is increasingly relevant. The growth in popularity associated with resource selection functions, such as the generalized linear mixed models implemented here, is a testament to such a focus (e.g., Gillies et al. 2006, Johnson et al. 2006). Thus, we should not expect all management actions to result in equivalent effects when operating in a highly heterogeneous environment. Hierarchical models lend themselves well to exploring complex interactions across multiple data sets or spatial scales, particularly when there is need to account for variation and uncertainty at the respective levels (Gelman et al. 2014). While the methods outlined here represent only one of many potential approaches, such models can be extended to evaluate the match between management action and objectives in a variety of circumstances where space is an important driver of management success. For example, we recognize the potential value in considering such models

within the context of restoration ecology (e.g., riparian restoration or animal reintroductions), habitat management (e.g., landcover modification or enhancement), or population regulation (e.g., ungulate management to reduce overbrowsing/grazing). By integrating resource selection data as we do here, or through incorporating demographic data, we can begin to quantify the relative impacts of spatially explicit management actions so that we may arrive at an unbiased understanding of efficacy.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1686/full>

DATA AVAILABILITY

Data available from GitHub: <https://doi.org/10.5281/zenodo.1135370>.