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RESEARCH ARTICLE

Modelling the distribution and intraguild associations of an understudied mesocarnivore across the contiguous United States

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Abstract

Aim: Understanding the range-wide distribution and abundance of species is critical for their conservation and management. Grey foxes (*Urocyon cinereoargenteus*) are an understudied, low-density mesocarnivore with a broad geographic range. However, the factors that underlie this broad distribution are poorly understood and large-scale analyses of this species' range and ecological niche are lacking.

Location: We modelled the probability and intensity of site use for grey foxes at two spatial scales using a coordinated survey of 1485 camera traps across the contiguous United States in 2019.

Methods: We used Bayesian occupancy modelling and post hoc species interaction comparisons to evaluate factors hypothesized to affect grey fox site use, including habitat, anthropogenic effects, and intraguild interactions.

Results: Our results showed that the presence of bobcats (*Lynx rufus*) and striped skunks (*Mephitis mephitis*), as well as forest variables, had positive associations with grey fox site use. Surprisingly, we found no support for negative effects on grey fox space use from dominant competitors (coyotes, *Canis latrans*, or pumas, *Puma concolor*), and a complete lack of effects from urbanization metrics and gross primary productivity. We did, however, find a consistent negative association with red foxes (*Vulpes vulpes*), which is the most ecologically and morphologically similar competitor of grey foxes.

Main conclusions: Taken together, these results imply that grey fox distribution is not limited by dominant carnivores or anthropogenic pressure. Rather, this species seems to occupy a unique niche across its broad range by exploiting diverse forest habitats shared with less ecologically similar competitors (striped skunks and raccoons, *Procyon lotor*), while being somewhat limited by a competitor occupying a similar ecological niche (red foxes). Our study highlights the value of broad-scale approaches for evaluating factors influencing the distribution and abundance of understudied species, as local dynamics might fail to manifest across geographic ranges.

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KEYWORDS

camera traps, carnivore, competition, distribution, grey fox, occupancy modelling, site use, suppression, *Urocyon cinereoargenteus*

1 | INTRODUCTION

Understanding the range-wide distribution and abundance of species is important for their conservation and management (Fryxell et al., 2014; Guisan & Thuiller, 2005). Distribution and abundance are shaped by variation in aspects of a species' ecological niche across its range, including habitat suitability and access to resources such as food, water, and cover (Peterson et al., 2011). Among mammalian carnivores, the ecological niche is further shaped by several additional key factors, including intraguild competition and negative effects from anthropogenic disturbance and development (Moll et al., 2018; Prugh & Sivy, 2020; Wang et al., 2015). Niche selection is also a hierarchical process, with selection for different resources at different scales (Johnson, 1980). A key challenge in understanding carnivore distribution and abundance is disentangling the relative contribution of these many factors across the broad spatial scales that carnivores tend to inhabit (Crooks et al., 2010; Linnell & Strand, 2000). Effectively addressing this challenge is critical given the decline of many carnivore species and the shifting community dynamics among carnivore guilds due to apex carnivore losses and associated trophic downgrading (Estes et al., 2011; Prugh et al., 2009; Ripple et al., 2014). Despite recent increased research effort to address this challenge for several large carnivore species (e.g., wolves *Canis lupus* and pumas *Puma concolor*; Ripple et al., 2014), there remain substantial knowledge gaps for many species, especially cryptic and low-density mesocarnivores (Allen et al., 2021; Moll et al., 2016).

Grey foxes (*Urocyon cinereoargenteus*) are a low-density and widespread but understudied mesocarnivore (Allen et al., 2021). Grey foxes are an adaptable species, being found in many temperate and tropical habitats, and ranging from Canada south into Central America. Grey foxes have a diverse diet, including fruits, small prey, and carrion, that is variable geographically and seasonally (Harmsen et al., 2019; Harrison, 1997). Robust population assessments are lacking for grey foxes (Allen et al., 2021), but the local abundance of populations appears to vary considerably across their range. More importantly, grey foxes are thought to be declining in some parts of their range (Bauder et al., 2021; Egan et al., 2021) and numerous state-level monitoring programmes indicate variable but generally downward population trends over the last several decades (e.g., Bauder et al., 2020; Conlee et al., 2019). These declines are possibly due to reductions in suitable habitat (Lesmeister et al., 2015), increases in anthropogenic disturbance (Ordeñana et al., 2010), or interactions with dominant carnivores (Egan et al., 2021). However, evaluations of the relative contribution of these factors across broad scales are lacking. In particular, continent-wide analyses have never been attempted with grey foxes despite the potential for elucidating these factors and contributing to the management and conservation of this species.

Given their adaptable and mobile nature, there are likely many environmental factors (i.e., habitat availability and increasing anthropogenic development) that could be affecting the range-wide distribution of grey foxes. Grey foxes are associated with a diversity of habitats throughout their range, with the one constant being a positive correlation with forested areas (Allen et al., 2021). Grey foxes often use forests that are open (Borchert, 2012) and have a preference for edge habitat (Davis et al., 2011; Harmsen et al., 2019). Yet much is unknown regarding the types of forests that grey foxes prefer or whether their distribution might be affected by the landscape characteristics of forest configuration (e.g., patch size). Their relationship with anthropogenic activity and development is even less clear, with several studies showing that grey foxes often have negative relationships with development (Lombardi et al., 2017; Nickel et al., 2020; Ordeñana et al., 2010), while others suggest little avoidance of development (Harrison, 1997; Riley, 2006).

As a mesocarnivore, intraguild interactions are also likely an important factor driving the distribution of grey foxes, as they can be killed or have their populations suppressed by larger carnivores (Donadio & Buskirk, 2006; Henke & Bryant, 1999; Lesmeister et al., 2015; Moll et al., 2021). While coyotes (*Canis latrans*) are generally thought to have negative effects on grey foxes, statistically the effects are often weak or not significant (see review in Allen et al., 2021). Results are similarly equivocal for bobcats (*Lynx rufus*) and red foxes (*Vulpes vulpes*) (Allen et al., 2021), although coyotes and bobcats are often a leading cause of predation-based mortalities (Farias et al., 2005; Weston & Brisbin, 2003). At the same time, grey foxes are often found to benefit from apex carnivores, such as pumas and grey wolves, that limit coyote abundance or distribution and release grey foxes from competition (Levi & Wilmsers, 2012; Newsome & Ripple, 2015). These equivocal findings are representative of a broader knowledge gap in carnivore community dynamics, namely, the relative influence of negative species interactions versus that of humans and habitat (Jachowski et al., 2020; Linnell & Strand, 2000; Moll et al., 2018).

Here, we address the complexities and uncertainties regarding grey fox distribution described above by analysing data from a coordinated survey of camera traps across the contiguous United States in 2019. We used Bayesian occupancy modelling to determine grey fox probability and intensity of site use at two spatial scales (100 m representing immediate camera site and 1 km representing a broader area of selection around the camera site). In the modelling, we included the major factors that we *a priori* hypothesized would affect grey fox distribution, including habitat, anthropogenic effects, and other carnivores (Table 1). Additionally, we used the posterior draws of our occupancy model to determine the effects of carnivores and their interactions on the probability of site use by grey foxes. Our analyses shed light on the relative importance of these

TABLE 1 The a priori covariates we considered for our occupancy models, including a description and our hypothesis/reason for including in the model

| Variables | Description | Hypothesis/reason | 100 m | 1 km |
|--|--|---|-------|------|
| Trap nights | The number of nights each camera trap site was active | Animals can be detected more often when monitored over longer time periods | | |
| Population density | The number of people, from Doxsey-Whitfield et al. (2015) | Grey foxes are positively affected by greater numbers of people (Nickel et al., 2020; Rota et al., 2016) | | |
| Housing density | The number of houses, from Radeloff et al. (2005) | Grey foxes are negatively affected by greater building densities (Lombardi et al., 2017; Nickel et al., 2020) | | |
| Impervious cover | Per cent of land cover that is impervious surface, from Homer et al. (2020) | Grey foxes are negatively affected by greater percentages of impervious cover (Ordeñana et al., 2010) | | |
| Road density | Number of roads, from Meijer et al. (2018) | Grey foxes are negatively affected by greater densities of roads (Lombardi et al., 2017) | | |
| Gross primary productivity | Proportion of normalized difference vegetation index (NDVI), from Hobi et al. (2017) | Mammals are often more abundant in areas with greater productivity (Willig et al., 2003) | | |
| Latitude | The latitude of a site | To control for potential spatial autocorrelation due to unmodelled factors (Rota et al., 2016) | ψ | |
| Longitude | The longitude of a site | To control for potential spatial autocorrelation due to unmodelled factors (Rota et al., 2016) | ψ | |
| Bobcat abundance | The capture rate of bobcats | Bobcats can have negative (Atwood et al., 2011) or positive (Rota et al., 2016) effects on grey foxes | ψ | ψ |
| Coyote abundance | The capture rate of coyotes | Coyotes often negatively affect grey foxes (Atwood et al., 2011; Donadio & Buskirk, 2006; Moll et al., 2021) | | |
| Puma abundance | The capture rate of pumas | Pumas often have a positive effect on grey foxes by releasing suppression by coyotes (Lesmeister et al., 2015; Wang et al., 2015) | | |
| Raccoon abundance | The capture rate of raccoons | As a common competitor, raccoons may negatively affect grey foxes (Bauder et al., 2021) | | |
| Red fox abundance | The capture rate of red foxes | Red foxes often have positive associations with grey foxes (Lesmeister et al., 2015; Rota et al., 2016) | | |
| Striped skunk abundance | The capture rate of striped skunks | As a common competitor, skunks may outcompete and negatively affect grey foxes (Bauder et al., 2021) | ψ | ψ |
| Deciduous, mixed forest, and total forest cover | The total size of each of wet forest, deciduous forest, and mixed forest, from Homer et al. (2020) | Grey foxes are often associated with various forest habitats (Allen et al., 2021; Borchert, 2012; Davis et al., 2011; Harmsen et al., 2019) | p | |
| Deciduous, mixed forest, and total forest edge | The density of edge habitat (m/ha) of each of wet forest, deciduous forest, and mixed forest, from Homer et al. (2020) | Grey foxes often use edge habitats (Davis et al., 2011; Harmsen et al., 2019) | ψ | ψ |
| Deciduous, mixed forest, and total forest patch size | The patch size of all forest types, from Homer et al. (2020) | Because grey foxes are associated with forest habitats, they will prefer areas with larger patch sizes | p | p |

Note: We extracted covariate data for our models at two scales: 100 m and 1 km buffer around each site. We extracted landscape variables using ArcMap v10.8 (ESRI, Redlands, CA), QGIS v3.12 (QGIS Development Team), and RStudio (R Core Team, 2021). We note which variables were used in our final models for probability of site use (ψ) and the intensity of site use (p) at both scales (100 m and 1 km).

factors for the distribution of grey foxes, with implications for the management and conservation of this understudied and at-risk mesocarnivore across their range.

2 | METHODS

2.1 | Study area

We used a network of camera traps distributed across the contiguous United States as part of the Snapshot U.S.A. 2019 campaign (Cove et al., 2021). The camera traps were part of a coordinated survey of 1,512 individual camera trap sites from 107 study arrays (Figure 1), that was active from August 17, 2019, to November 24, 2019 (with 98.0% of activity in the 10-week period from 25 August 2019, to 9 November 2019). There were camera sites in all lower 48 states ranging from 25.17° to 48.14° latitude and from -124.02° to -69.10° longitude (Figure 1). Bioclimatic conditions, habitat, and anthropogenic development all varied strongly across this broad study area. Generally, the eastern United States is characterized by relatively high forest cover that diminishes moving westward into the great plains, which are dominated by agriculture interspersed with forests, anthropogenic development, and grasslands (Figure 1). The western United States contains several major mountain ranges as well as more humid coastal areas that experience relatively mild and stable year-round temperatures. Thus, overall, the Snapshot U.S.A. camera trap arrays capture the mammal communities in all

major habitat, climate, landscape, and disturbance regimes across the country.

2.2 | Data collection

Camera trap arrays were established and managed by individual participants in Snapshot USA, with the goal of obtaining comparable mammal community data across the continent. All specifics on establishment arrays and camera models are reported in (Cove et al., 2021). Briefly, each array was active for a minimum of 400 trap nights and cameras spaced 200–5000 m apart from one another (although these parameters were not always possible due to logistical or planning constraints). Cameras were placed ~30–50cm high and programmed to take 1–10 photographs per detection without a refractory period. The camera traps used all met minimum standards with fast trigger speeds and high-resolution photographs. All resulting data from camera traps were managed through the eMammal Data Management System (emammal.si.edu) and were reviewed in a secondary process by at least one expert. We aggregated photographs of a given species into independent events when they were greater than one-minute apart. We controlled for variation in camera sampling of arrays by including survey effort (as trap nights) in our modelling both directly and indirectly by incorporating it into the calculation of capture rate for interacting carnivores and by varying the number of replicate surveys per site to match the total number of trap nights each site was active for, respectively.

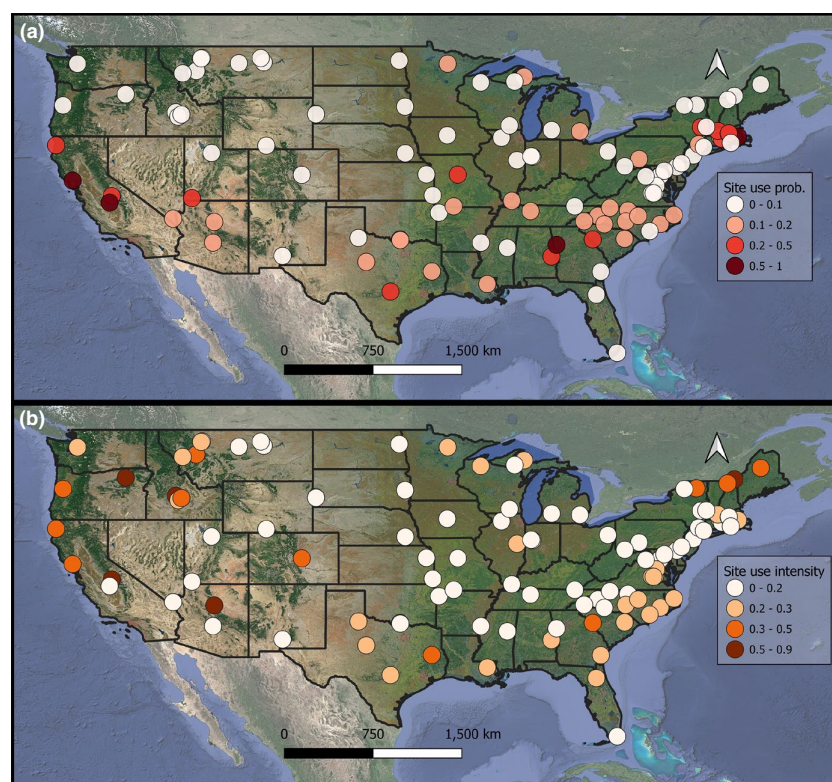


FIGURE 1 Model-predicted probability (ψ) and intensity (p) of site use for grey foxes across the United States. Models were fit to data collected from 1485 camera traps deployed across 107 study sites in fall 2019. Each circle represents the mean predicted value for the array of all cameras at a study site

We extracted covariate data for our occupancy models at two scales (100 m and 1 km buffer around each site). We extracted landscape variables using ArcMap v10.8 (ESRI, Redlands, CA), QGIS v3.12 (QGIS Development Team), and the packages *sf*, *raster*, and *landscapemetrics* in RStudio (Hesselbarth et al., 2019; Hijmans & van Etten, 2016; Pebesma, 2018; R Core Team, 2021). The full description of our covariates and the justification for including them in the models are outlined in Table 1.

2.3 | Statistical analyses

We conducted our data analyses on a truncated portion of the 2019 Snapshot USA dataset (Cove et al., 2021). In total, we analysed data from 1,485 camera deployments across the contiguous 48 states for a total of 51,095 survey days (Supplemental Material 1). We used this dataset to craft detection histories for grey fox and other carnivore species that we *a priori* hypothesized would affect grey fox distribution, including bobcat, puma, coyote, northern raccoon (*Procyon lotor*; hereafter referred to as “raccoon”), red fox, and striped skunk (*Mephitis mephitis*). We prepared species-specific detection histories for this dataset for occupancy modelling, with each replicate sampling occasion consisting of seven consecutive camera days, which helps reduce bias in occupancy estimates, especially when movement around a particular sampling site is non-random at shorter temporal scales (e.g. carnivores traversing entire home ranges (Kendall & White, 2009)). We performed these analyses using the *camtrapR* package version 2.0.3 in program R version 4.02 (Niedballa et al., 2016; R Core Team, 2021).

2.4 | Occupancy modelling

We modelled grey fox distribution across the contiguous United States using a single species, single season Bayesian occupancy model (Kéry & Royle, 2015; MacKenzie et al., 2017). Following the recommendations of MacKenzie et al. (2017), instead of estimating the proportion of total study area occupied by each species and the detection probability of a species, respectively, we defined the parameters of interest (occupancy and detection probability) as the probability of site use (ψ) and the intensity of site use (p ; i.e. the probability a species returns to a site, given use), respectively, to control for the potential bias that can come from closely spaced cameras that potentially violate spatial independence (Kéry & Royle, 2008; MacKenzie et al., 2002, 2017; Suraci et al., 2021). Multiple covariates were correlated with other predictors (Pearson's $r > 0.7$). Therefore, to craft our final model at each scale (100 m and 1 km), we started by first running univariate models on intensity of site use while holding site use probability constant, retaining predictors that produced a significant signal (as indicated when a beta coefficient's 95% Bayesian credible interval [CI] did not overlap 0). If collinear predictors both significantly affected intensity of site use, we excluded the one whose beta coefficient was smaller in magnitude.

These predictors included the capture rate (number of captures per trap night) of all interacting carnivore species hypothesized to influence grey foxes, as mentioned above (Table 1). We elected to use capture rate instead of the multispecies occupancy model described by Rota et al. (2016) to reduce overparameterizing a model with limited sample sizes and naïve occupancy values for many of the interacting species, as well as to improve convergence of model parameters, parameter estimate precision, and model run time (Kéry & Royle, 2015; Naidoo & Burton, 2020). We then sequentially removed all non-significant predictors until only those that significantly predicted grey fox intensity of site use remained. We then repeated this process on the site use probability parameter using the final intensity of site use model from the first step. We included latitude and longitude on site use probability to account for the spatial clustering within the dataset (Cove et al., 2021). Before analysis, we standardized each continuous covariate to have a mean = 0 and standard deviation = 1 to improve numerical optimization and allow for direct comparison of beta coefficients (Schielzeth, 2010). We assessed model fit using Bayesian p -values calculated from observed and modelled data (Hobbs & Hooten, 2015; Suraci et al., 2021). We calculated these values using chi-squared discrepancy statistics (Kéry & Shuab, 2012; Suraci et al., 2021).

We conducted all analysis by estimating posterior distributions for all coefficients of interest using Markov chain Monte Carlo (MCMC) methods implemented in JAGS through program R using the *R2Jags* and *jagsUI* packages (Kellner et al., 2019; Su & Yajima, 2015). For each model, we ran three chains in parallel, each consisting of 50,000 iterations, where we discarded the first 25,000 draws from each chain as burn-in. We applied a thinning rate of 10 to each chain, resulting in 7500 total samples retained to craft the posterior distributions of each parameter. We used flat uniform distributions from -10 to 10 as priors for each beta coefficient. We assessed parameter convergence by visually inspecting individual traceplots and by calculating the Gelman-Rubin statistic, where values <1.1 indicate convergence across chains (Gelman, 2004).

2.5 | Interspecific interactions

Each draw from the MCMC algorithm represents a separate estimate for all parameters, including the site-specific predictions of grey fox site use as a function of environmental covariates and carnivore capture rates at each of the two spatial scales. These predictions of site use further account for imperfect detection, that is a grey fox used a site but was not detected on camera (Rich et al., 2016; Zipkin et al., 2010). Re-running our occupancy models using only the significant environmental predictors (and excluding the significant carnivore capture rates), we then used the mean estimate for each site from the MCMC chains as our response variable and modelled the effect of the detection of other carnivore species on grey fox site use probability using an ANOVA, including interactions terms for multiple carnivore species. We performed this second analysis step because in addition to understanding the additive effects of

individual carnivore species' capture rates on grey fox site use probability and intensity, we were also interested in understanding the interactions of carnivore assemblage on grey fox site use probability. Furthermore, we wanted to use a method that allowed us to measure the magnitude of these effects and determine how much grey fox site use probability changes in response to different carnivore assemblages. Specifically, we ran (1) a "competitor" model, including striped skunk, red fox, and raccoon detection, as well as interactions across the three species and (2) a "dominant" model, including puma, coyote, and bobcat detection/non-detection, as well as interactions across the three species. We assessed significance in these models at $\alpha = .05$, and a Tukey's honest significant difference test was performed *post hoc* to assess the magnitude difference in grey fox site use probability across states of detection/non-detection.

3 | RESULTS

We recorded 466 total detections of grey foxes across the study area. Grey foxes were detected at 107 camera traps, resulting in a naïve site use probability estimate of 0.07. We also recorded a total of 13,602 detections of the six interacting carnivore species included in our analysis. Detections ranged from 29 of puma to 8928 of raccoon, while naïve site use probabilities ranged from 0.02 for puma to 0.44 for raccoon (Table 2).

3.1 | Occupancy model

Our occupancy model for grey foxes at the 100 m resolution spatial scale had a robust fit between modelled and observed data with a Bayesian p value of .41 (Supplementary Material 2a). Estimated grey fox ψ was 0.10 (CI = 0.07–0.12), resulting in a mean estimate of 177.94 used sites (CI = 152.00–210.00). ψ was positively affected by bobcat capture rate ($\beta = .33$, CI = 0.12–0.57), striped skunk capture rate ($\beta = 1.06$, CI = 0.40–1.76), and mixed deciduous forest edge ($\beta = .55$, CI = 0.32–0.77). No measured predictors had a negative effect on grey fox ψ (Figure 2a).

TABLE 2 The total detections, capture rate (average number of detections per 100 trap nights), and naïve site use probability (occupancy) of each carnivore species in our analyses

| Species | Detections | Capture rate | Naïve site use probability |
|------------------|------------|--------------|----------------------------|
| Grey fox | 466 | 0.91 | 0.07 |
| Bobcat | 352 | 0.69 | 0.1 |
| Coyote | 2355 | 4.61 | 0.36 |
| Puma | 29 | 0.06 | 0.02 |
| Northern Raccoon | 8928 | 17.47 | 0.44 |
| Red Fox | 1569 | 3.07 | 0.12 |
| Striped Skunk | 369 | 0.72 | 0.08 |

Grey fox p in our 100 m spatial scale model was estimated to be .10 (CI = 0.04–0.18). p was negatively affected by both deciduous forest cover ($\beta = -.49$, CI = -0.86 to -0.13) and mixed deciduous forest patch size ($\beta = -3.89$, CI = -7.46 to -1.41), and p was positively affected by both total forest cover ($\beta = .47$, CI = 0.18–0.76) and total forest patch size ($\beta = .85$, CI = 0.45–1.29; Figure 3a).

Our occupancy model for grey foxes at the 1 km resolution spatial scale had an excellent fit between modelled and observed data Bayesian p value of .50 (Supplementary Material 2b). Grey fox ψ was estimated to be 0.08 (CI = 0.07–0.11), resulting in a mean estimate of 163.68 used sites (CI = 141.00–191.00). ψ under this model was also positively affected by bobcat capture rate ($\beta = 0.33$, CI = 0.14–0.55) and striped skunk capture rate ($\beta = 1.08$, CI = 0.49–1.75), as well as total forest edge ($\beta = 0.63$, CI = 0.37–0.90). As with the 100 m resolution model, no measured predictors negatively affected grey fox ψ (Figure 2b).

Grey fox p in the 1 km spatial scale model was estimated to be 0.12 (CI = 0.05–0.22). p was positively affected by total forest patch size ($\beta = 1.27$, CI = 0.91–1.66) but negatively affected by mixed deciduous forest patch size ($\beta = -4.30$, CI = -7.74 to -1.77 ; Figure 3b).

3.2 | Interspecific interactions

In interactions with competitive carnivores, grey fox ψ was positively associated with detection of both raccoons and striped skunks, and these associations were statistically significant at both scales (Table 3; Figure 4a). Conversely, grey fox ψ had a significant negative association with red fox detection at both spatial scales (Table 3; Figure 4a). There was also a significant interactive association of raccoon detection on grey fox ψ that was dependent on red fox detection at both spatial scales (Table 3). This positive association between raccoon detection and grey fox ψ disappeared when red foxes were also detected (Table 3). Specifically, grey fox ψ was lower in areas where both raccoons and red foxes were detected compared to areas where only raccoons were detected (mean difference = -0.09 , CI = -0.04 to -0.15 , $p = <.01$ at both spatial scales; Table 3). Similar to raccoons, the positive affect of striped skunk detection on grey fox ψ disappeared when red foxes were also present (Table 3). Grey fox ψ decreased in areas where both striped skunks and red foxes were detected as opposed to where only striped skunks were detected (mean difference_{100 m} = -0.32 , CI = -0.17 to -0.47 ; mean difference_{1 km} = -0.33 , CI = -0.18 to -0.47). Finally, there was no evidence to suggest that grey fox ψ was associated with a three-way interaction among competing carnivores ($f_{100 m} = 0.02$, $p = .70$; $f_{1 km} = 0.01$, $p = .70$) at either scale (Figure 4a). Additional details of these results are provided in Supplemental Material 3.

In interactions with dominant carnivores, grey fox ψ was positively associated with bobcat detection at both scales (Table 3; Figure 4b). There was no difference in estimated grey fox ψ with coyote detection or puma detection (Table 3). Grey fox ψ was higher in areas with bobcat detection vs. areas with coyote detection, with a mean difference of 0.17 (CI = 0.07–0.26, $p = <.01$) in the 100 m

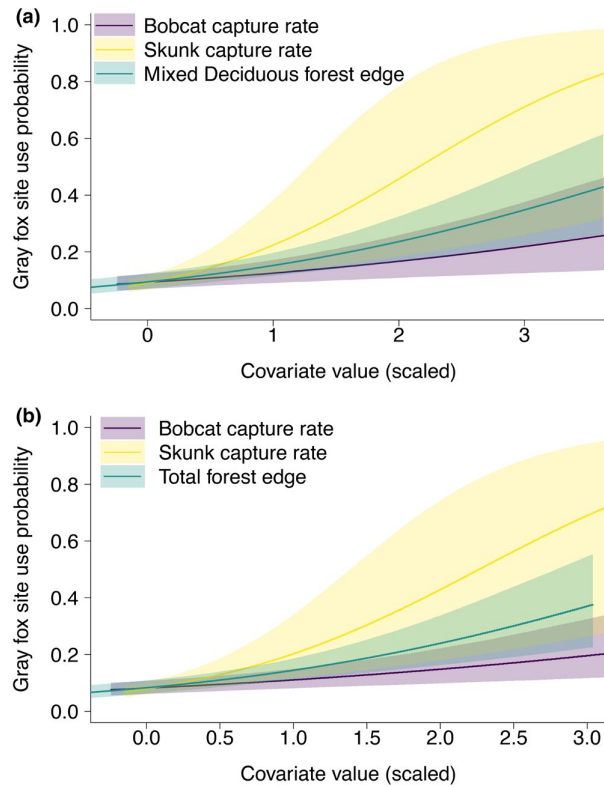


FIGURE 2 The relationship of statistically significant factors with the probability of site use (ψ) for grey foxes at the (a) 100 m and (b) 1 km scales

resolution model and 0.16 (CI = 0.07–0.26, $p = <.01$) in the 1 km resolution model. There was a similar positive effect in areas with bobcat detection vs. areas with puma detection ($\text{mean}_{100\text{ m}} = 0.25$, CI = 0.08–0.41, $p = <.01$; $\text{mean}_{1\text{ km}} = 0.22$, CI = 0.06–0.39, $p = <.001$). Finally, there was little evidence to suggest that grey fox ψ was associated with a three-way interaction amongst dominant carnivores at either scale ($f_{100\text{ m}} = 2.71$, $p = .10$; $f_{1\text{ km}} = 2.67$, $p = .10$). Additional details of these results are provided in Supplemental Material 4.

4 | DISCUSSION

Grey fox are a low-density species with populations that are declining in some areas (Bauder et al., 2021; Egan et al., 2021), while remaining robust in others, suggesting there are local or regional factors that can affect their presence and abundance. Here, we investigated these dynamics on a continental-scale and found that the presence of certain mesocarnivores and forest variables were positively related to the probability (ψ) and intensity of site use (p) by grey foxes. Surprisingly, we found no support for negative effects on grey foxes from coyotes or pumas, which are both dominant competitors that kill grey foxes (Allen et al., 2015; Donadio & Buskirk, 2006; Henke & Bryant, 1999). Similarly, grey foxes did not respond either positively or negatively to urbanization metrics or gross primary

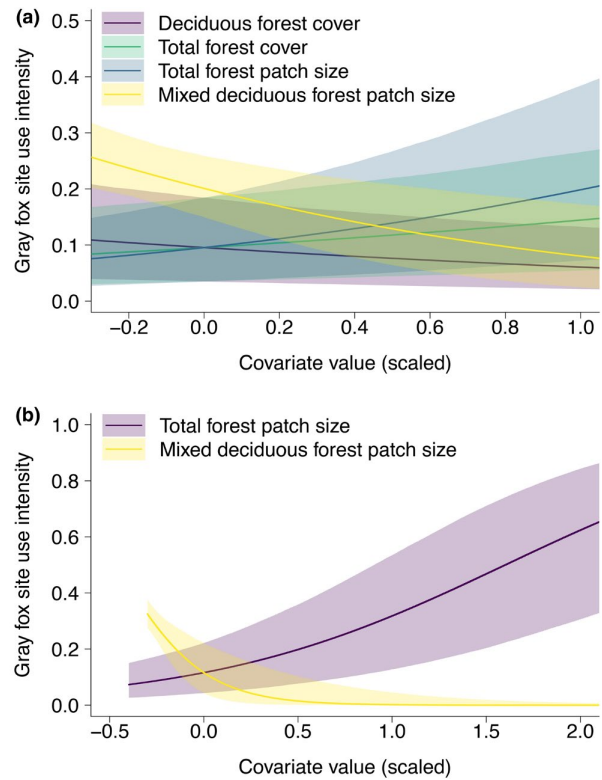


FIGURE 3 The relationship of statistically significant factors with the intensity of site use (p) for grey foxes at the (a) 100 m and (b) 1 km scales

productivity. We did, however, find a consistent negative association with red foxes, which are the most ecologically and morphologically similar competitor of grey foxes. Taken together, these results imply that grey fox distribution is not limited by dominant carnivores or anthropogenic pressure. Rather, this species seems to occupy a unique niche across its broad range by exploiting diverse forest habitats shared with less ecologically similar competitors (striped skunks and raccoons) that is somewhat limited by the presence of red foxes. This study further highlights the value of broad-scale approaches for evaluating factors influencing the distribution and abundance of understudied species, as local dynamics may fail to manifest across geographic ranges.

Grey fox site use was affected by interactions with dominant species, but not as we expected. As a mesocarnivore, grey foxes are often killed by dominant carnivores (Farias et al., 2005; Weston & Brisbin, 2003), and sometimes have their populations suppressed (Egan et al., 2021; Henke & Bryant, 1999; Moll et al., 2021). However, we did not find any negative effects on grey foxes from either coyotes or pumas. Instead, grey fox ψ and p were positively affected by bobcats. Most studies exploring spatial or temporal interactions between grey foxes and coyotes found evidence of negative effects of coyotes on grey foxes (see review by Allen et al., 2021); however, the negative effects of coyotes were often weak or not statistically significant. Our results similarly

TABLE 3 Sympatric carnivore effects on grey fox site use probability

| 100 meter scale | | | | |
|-------------------|----------------------------|--------------------------|----------------------------|----------------------------|
| Competitors | | | | |
| Species | Change in ψ | Interaction with Raccoon | Interaction with Skunk | Interaction with Red Fox |
| Red Fox | -0.07 (-0.10 to -0.03) | -0.02 (-0.15 to 0.10) | -0.07 (-0.21 to 0.07) | — |
| Raccoon | 0.06 (0.04 to 0.09) | — | 0.18 (0.10 to 0.26) | -0.09 (-0.15 to -0.04) |
| Striped Skunk | 0.16 (0.11 to 0.20) | 0.11 (-0.01 to 0.22) | — | -0.32 (-0.47 to -0.17) |
| Dominants | | | | |
| Species | Change in ψ | Interaction with Coyote | Interaction with Puma | Interaction with Bobcat |
| Bobcat | 0.15 (0.11 to 0.19) | -0.03 (-0.15 to 0.08) | 0.00 (-0.22 to 0.23) | — |
| Coyote | 0.00 (-0.02 to 0.03) | — | -0.03 (-0.18 to 0.12) | 0.13 (0.06 to 0.20) |
| Puma | -0.06 (-0.16 to 0.03) | 0.12 (-0.16 to 0.39) | — | 0.25 (-0.02 to 0.52) |
| 1 kilometer scale | | | | |
| Competitors | | | | |
| Species | Change in ψ | Interaction with Raccoon | Interaction with Skunk | Interaction with Red Fox |
| Red Fox | -0.07 (-0.10 to -0.03) | -0.03 (-0.15 to 0.10) | -0.07 (-0.21 to 0.07) | — |
| Raccoon | 0.06 (0.04 to 0.09) | — | 0.18 (0.11 to 0.26) | -0.09 (-0.15 to -0.04) |
| Striped Skunk | 0.17 (0.12 to 0.21) | 0.09 (-0.02 to 0.21) | — | -0.33 (-0.47 to -0.18) |
| Dominants | | | | |
| Species | Change in ψ | Interaction with Coyote | Interaction with Puma | Interaction with Bobcat |
| Bobcat | 0.15 (0.11 to 0.19) | -0.03 (-0.14 to 0.08) | 0.02 (-0.20 to 0.24) | — |
| Coyote | 0.01 (-0.02 to 0.03) | — | -0.01 (-0.16 to 0.14) | 0.13 (0.06 to 0.20) |
| Puma | -0.05 (-0.14 to 0.05) | 0.12 (-0.15 to 0.40) | — | 0.24 (-0.02 to 0.51) |

Note: Values are mean estimates with ranges in parentheses representing 95% confidence intervals. Interaction effects represent the difference in grey fox site use probability (ψ) between sites where both competitors and dominants were detected vs. when only the interacting species was detected. Bolded values represent estimates whose 95% confidence interval does not overlap 0.

showed little effect of coyotes on grey foxes, despite known predation (Farias et al., 2005; Weston & Brisbin, 2003). The positive effects of bobcats were also surprising, as most previous studies have reported bobcats having negative effects on grey foxes, although the effects were often minimal (Allen et al., 2021; Moll et al., 2021). Together, these observations underscore the complexity of interactions among carnivores, especially across large spatial scales.

Cascades within carnivore guilds are known, including just within the canid guild (Levi & Wilmers, 2012; Moll et al., 2021; Newsome & Ripple, 2015), but we did not find enough evidence in our models to suggest that grey foxes were associated with three-way interaction cascades amongst dominant carnivores at either scale (Table 3; Figure 4b). While most of these cascades include grey wolves, which have a positive effect on grey foxes by suppressing coyotes (Levi & Wilmers, 2012; Newsome & Ripple, 2015), we did not have sufficient grey wolf detections to include in models. Pumas also often have either positive effects, by directly limiting coyotes at feeding sites (Allen et al., 2015) and communication sites (Allen et al., 2017), or neutral effects (Davis et al., 2011) on grey foxes. Because our dataset was limited to 29 puma detections, our results do not preclude

the possibility of cascades among carnivores (e.g. Levi & Wilmers, 2012; Moll et al., 2021; Newsome & Ripple, 2015), and multi-species interactions among carnivores should continue to be studied.

Despite the lack of evidence for cascading relationships, our results do indicate the importance of interactions or associations with other mesocarnivores. Overall, it was red foxes, the most ecologically similar species to grey foxes, that had the largest negative effects, even though previous studies have found that red foxes often have equivocal effects on occupancy of grey foxes (Lesmeister et al., 2015; Rota et al., 2016). The ψ and p at both scales was also positively affected by raccoons and striped skunks. This may be because all three mesocarnivores may be more prevalent in areas with fewer dominant carnivores, regardless of whether any three-way interactions including dominant carnivores were significant (Crooks et al., 2010). But most importantly, we found that the positive effects of raccoons and striped skunks disappeared when red foxes were also detected at a site. These community dynamics may be indicative of the unique niche used by grey foxes across their range that shifts when their most similar ecological competitor (red foxes) is present. This finding illustrates the significance of considering complex interspecific interactions in conservation and management planning

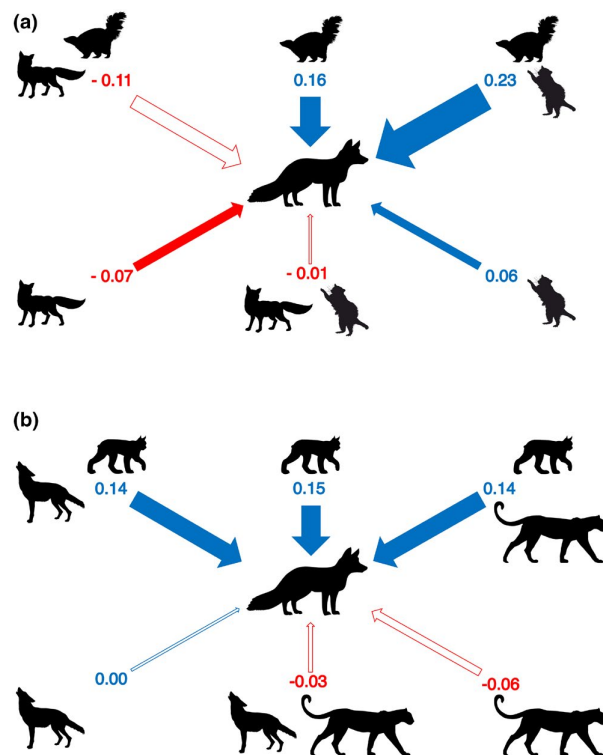


FIGURE 4 Carnivore effects on grey fox site use probability (ψ), representing species or species groups detected (a. competitors, b. dominants), at the 100 m scale. Arrows and numbers represent the magnitude of change in grey fox site use probability (between sites with the species or species groups detected vs. sites without these species or groups detected). Red arrows represent negative changes and blue represent positive changes, with filled arrows representing significant differences and hollow arrows represent non-significant differences

because decisions based upon simpler metrics (e.g. habitat alone) could be ineffective due to oversimplifying these subtle but important population dynamics.

Grey foxes are often thought of as a forest dependent species (Allen et al., 2021; Borchert, 2012; Davis et al., 2011; Harmsen et al., 2019), and while forest covariates were important in our results, their effects were nuanced. ψ was positively affected by mixed deciduous forest edge at the 100 m scale and total forest edge at the 1 km scale. This supports results from previous studies that show grey foxes use of edge habitats (Davis et al., 2011; Harmsen et al., 2019), as well as heterogeneous landscapes that are likely indicative of edge habitat (Lesmeister et al., 2015). The effects of habitat on p was even more nuanced, with total forest cover and patch size having positive effects, but deciduous cover and patch size having negative effects. Lesmeister et al. (2015) reported a negative association between grey foxes and hardwood forests in Illinois, while other studies have shown grey fox selection for deciduous forests varies by spatial scale and season (Chamberlain & Leopold, 2000; Deuel et al., 2017; Temple et al., 2010). Previous studies have sometimes

indicated limited or no association with forest cover (Rich et al., 2018) and canopy cover (Davis et al., 2011).

Wildlife assemblages across the world are often affected by human development and activity (Crooks et al., 2010; Suraci et al., 2021) and gross primary productivity (Willig et al., 2003), but none of these factors affected the ψ or p of grey fox site use in our analyses using sites from across the contiguous United States. Many studies have reported that anthropogenic development has a negative effect on grey foxes (Kowalski et al., 2015; Lombardi et al., 2017; Nickel et al., 2020; Ordeñana et al., 2010), yet other studies found that they use a range of human development intensities (Harrison, 1997; Kapfer & Kirk, 2012; Riley, 2006; Suraci et al., 2021) and that human activity has a positive effect on grey foxes (Nickel et al., 2020; Rota et al., 2016). These varying effects of anthropogenic development may be due to more complex factors, such as grey foxes using anthropogenic landscapes to avoid coyotes (Lesmeister et al., 2015; Wang et al., 2015). This may also reflect the complexity of habitat associations and niche of grey foxes that may be dependent on seasonality and variable resources or other factors such as prey base and competitors, and we encourage continent-wide surveys across multiple seasons and years as a next step.

Several limitations of the dataset and analyses could impact the conclusions of this research. First, while the broad nature of this study enabled a rigorous assessment of grey fox site use across North America, we acknowledge that there was variation in camera placement across the 107 arrays, most of which were sampled by individual research groups. Thus, it is possible that cameras could have been placed at sites that favoured co-occurrence of the carnivore guild studied here, such as natural areas within urbanized landscapes. However, the overall study design discouraged the targeting of specific landscape features (e.g. wildlife trails), while our dual-scale modelling approach evaluated both site-level and landscape-level habitat variation, thereby controlling for this potential limitation. Another potential limitation is the use of carnivore capture rates as covariates instead of a detection corrected measure of carnivore distribution. Without including a detection-corrected measure, we may have missed sites where the carnivore was present but not detected. However, capture rates have been found to correlate well with both species occupancy and relative abundance (MacKenzie et al., 2017; Zuckerberg et al., 2009) and can provide fine-scale estimates of hotspots of carnivore presence and activity. Furthermore, the relatively low naïve occupancy values we estimated for many of our interacting carnivore species would have made it difficult to detect a signal due to relatively high imprecision.

On a broader level, this study highlights the importance of large-scale analyses for clarifying species' niches and the associated factors driving their distribution and abundance (Angerbjörn et al., 2013). Many terrestrial carnivores are wide-ranging, highly mobile, and present in low densities, and local studies often report conflicting importance of factors shaping their niches and distributions (e.g. Moll et al., 2016). Further, the spatial scales at which carnivore conservation measures take place are often mismatched with the scales

of research ostensibly informing such measures (Bautista et al., 2021; Montgomery et al., 2018). These tendencies are further complicated by a tendency to simplify complex carnivore systems by focusing only on one or a few interspecific interactions (Montgomery et al., 2019; Prugh & Sivy, 2020). Here, we showed how grey foxes appear to be able to exist across various habitats and carnivore assemblages, indicating the breadth of their niche. At the same time, forest configuration and associations with other carnivores were among the most important factors shaping grey fox site use, but this may indicate a co-occurrence with this community assemblage rather than an attraction to these species (Zurell et al., 2018). Nonetheless, our results clearly indicate how nuanced factors and especially interspecific interactions can underlie carnivores' niches and distributions. Thus, broad-scale analyses incorporating such factors play a crucial role in informing conservation and management planning, especially for low-density carnivores.

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CONFLICT OF INTEREST

The authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The camera trap data from this manuscript are fully available from Snapshot U.S.A. (Cove et al., 2021) at <https://doi.org/10.1002/ecy.3353> and can be used freely by any scientist, and the covariate data we used in our models are available in Supplementary Material 1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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