Dependence of spatial scale in landscape associations with cause-specific predation of snowy plover nests

KRISTEN S. ELLIS\(^1\),\(^\dagger\) RANDY T. LARSEN,\(^2\) AND DAVID N. KOONS\(^3\)

\(^1\)Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523 USA
\(^2\)Department of Plant and Wildlife Sciences, Brigham Young University, Provo, Utah 84602 USA
\(^3\)Department of Fish, Wildlife, and Conservation Biology, and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA

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Abstract. Understanding relationships between habitat and ecological processes often depends on the spatial scale at which the landscape is measured. A common objective in studies of avian nesting ecology is to link habitat characteristics with nest predation for generating potential conservation and management strategies aimed at increasing avian reproductive success. Yet scale dependence likely plays a considerable role in these assessments, particularly when multiple species of nest predators are present. We identified nest predators of snowy plovers, a ground-nesting shorebird, and modeled predator-specific hazard rates of nest mortality in relation to the landscape at multiple spatial scales (200 m, 500 m, 1 km, 2.5 km, and 5 km) and at the nest site. We used a Bayesian latent indicator approach for weighting the influence of habitat across spatial scales and to gain insight into the hierarchical nature of how specific predators responded to the landscape when preying upon plover nests. We did not identify a common spatial scale that best predicted nest predation by all predators, though our results indicated that unfragmented playa and marsh habitats at large spatial scales reduced nest predation by all nest predators. Land cover features including grass, shrubs, human development, and open water elicited variable responses depending on the predator group, and predator groups responded at different spatial scales. Further, the spatial configuration of nests (nest dispersion) influenced nest predation by common ravens *Corvus corax* and foxes (kit fox *Vulpes macrotis* and red fox *Vulpes vulpes*), suggesting that certain predators develop a search image for nests. Our results illustrate that clarifying complex relationships between nest predation and habitat characteristics requires the incorporation of predator identity and scale dependence. Thus, management and conservation plans aiming to increase avian productivity by altering or restoring habitats will likely benefit from consideration of predator-specific patterns at multiple spatial scales.

Key words: Bayesian indicator variable; cause-specific mortality; hazard rates; remote cameras; shorebird; spatial scale.

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† E-mail: Kristensue.Ellis@gmail.com

INTRODUCTION

Wildlife species interact with and perceive the environment at different spatial scales, and thus, understanding ecological processes is inherently dependent on the spatial scale at which habitat structure is measured (Wiens 1989, Levin 1992). By evaluating species–habitat relationships at multiple spatial scales, one can identify the scale with the strongest effect and gain more relevant ecological inference (Morris 1987, Jackson and Fahrig 2015). For example, avian body size was...
shown to be positively correlated with the spatial scale at which species respond to the landscape structure, providing evidence that life-history traits can facilitate interactions with the environment (Thornton and Fletcher 2014). While the awareness of scale dependence in ecology exists, quantifying ecological processes at varying spatial scales has proven difficult and is often disregarded or over-simplified (Jackson and Fahrig 2015, Stuber et al. 2017). Further complexities can arise when linking relevant scales of the environment to ecological processes involving multiple interacting species (Chiavacci et al. 2018).

One scenario where dependence on spatial scale likely plays a considerable role is predation on avian nests, particularly when a diverse assemblage of predator species competes for a common set of nests (Ellis et al. 2020). Nest predation represents the greatest source of reproductive failure for most birds and may significantly influence their evolutionary life-history strategies and population dynamics (Ricklefs 1969, Martin 1995). A common objective in studies of avian nesting success is to link habitat features (e.g., amount of habitat edges, vegetation cover) to nest predation in order to generate potential management actions. Historically, the focus of such studies has been on a single spatial scale (e.g., nest-site, patch, or landscape), and relatively few have examined the effects of habitat on nest predation at multiple spatial scales (Chalfoun et al. 2002, Stephens et al. 2004). With respect to habitat fragmentation, nest predators may be more sensitive to habitat structure at the landscape scale (Stephens et al. 2004). Yet, the appropriate buffer width surrounding nests in which landscape components should be measured likely varies with specific nest predators and associated foraging behavior.

Conflating sources of predation may obscure predator-specific relationships with habitat and lead to inconsistent results across studies (Tewksbury et al. 1998, Benson et al. 2010, Lyons et al. 2015). For example, predator species that use habitat edge as foraging and movement corridors may encounter more nests in fragmented landscapes, resulting in lower nest survival (Lahti 2001, Batary and Baldi 2004, Stephens et al. 2004), but this relationship may be difficult to detect when predator identity is unknown (Tewksbury et al. 1998, Lahti 2001). Including predator identity has been recommended when assessing the relationship between habitat and nest predation (Phillips et al. 2003, Tewksbury et al. 2006, Lyons et al. 2015), and recent work has shown that this can lead to a better understanding of patterns of nest predation (Benson et al. 2010, DeGregorio et al. 2016, Chiavacci et al. 2018).

When predator identity is known via the use of remote cameras (e.g., McKinnon and Béty 2009, Ellis et al. 2018, Andes et al. 2019), variation in nest predation may be explained by considering multiple scales of the landscape (Chiavacci et al. 2018). The relationship between nest predation and habitat likely depends on the spatial scale that is relevant to specific predators because of varying body size, diet, foraging behavior, and habitat use (DeGregorio et al. 2016, Chiavacci et al. 2018). For example, mammalian meso-predators respond to habitat features at different spatial scales depending on body size and level of mobility (Gehring and Swihart 2003). However, mechanisms by which landscape features at different scales influence predator-specific nest mortality could also include alterations of predator behavior (smaller spatial scales), or the carrying capacity of landscapes for predators (larger spatial scales; Brown and Litvaitis 1995, Laidlaw et al. 2015, Chiavacci et al. 2018). Few studies have examined patterns of predator-specific nest predation at multiple landscape scales, yet evidence suggests that no single scale can best predict nest predation by all predators (Chiavacci et al. 2018). Thus, a formal accounting of the relationship between habitat features and nest predation by specific predators is needed for effective habitat-restoration and management programs (Clark and Nudds 1991, Norris 2004).

Shorebirds have experienced diminishing habitats and globally, many populations are declining (Colwell 2010, Andres et al. 2012, Studds et al. 2017, Murray et al. 2018). Impacts of habitat and reproductive failure have been identified as key issues constraining the sustainability of many shorebird populations (Colwell 2010, Andres et al. 2012). Thus, our goal was to evaluate the importance of habitat features at multiple spatial scales (from nest site to landscape) on predator-specific nest predation in snowy plovers Charadrius nivosus. Snowy plovers are a
shorebird of conservation concern throughout much of their range (e.g., the Pacific population is listed as threatened under the U.S. Endangered Species Act), with increased nest failure and habitat loss being identified as primary factors contributing to their decline (USFWS 2007). Rather than using model comparison to select a best spatial scale of association between habitat and animal fitness, we used a Bayesian latent indicator approach for weighting the influence across scales of habitat on cause-specific predation of snowy plover nests (Stuber et al. 2017). This method allowed us to evaluate multiple scales for each specific nest predator and gain insight into the hierarchical nature of how specific predators responded to the landscape when preying upon plover nests. Given the positive correlation between predator body size and space-use area in meso-predators (Gehring and Swihart 2003), we predicted that nest predation by larger-bodied mammalian predators (e.g., coyotes Canis latrans) would be influenced by habitat at larger scales because of their large home ranges and mobility, and smaller mammalian predators (e.g., red foxes Vulpes vulpes and kit foxes Vulpes macrotis) would conversely be influenced by habitat at smaller spatial scales. We also predicted that nest predation by mammalian predators would be higher compared to avian predators in more fragmented landscapes because habitat edges can serve as foraging corridors for meso-predators (Frey and Conover 2006). Lastly, we predicted that nest predation by avian predators would increase when vegetative cover was lower at the nest site because of their reliance on visual stimuli for foraging (Schmidt 1999).

Methods

Study areas

We collected data at two study areas in Utah, USA: western Utah, and Great Salt Lake (Fig. 1). Study areas within western Utah included Fish Springs National Wildlife Refuge (2011–2017), the United States Army Dugway Proving Ground (2011–2017), and Blue Lake (2016–2017). Snowy plover occupancy is low in western Utah and is associated with ephemeral water sources (Ellis et al. 2014). Yet, habitat loss and disturbance by humans is minimal in western Utah because breeding areas are remote or on military lands with restricted access. Fish Springs National Wildlife Refuge encompasses 36 km² of marsh habitat which is supplied by multiple thermal springs (Stolley et al. 1999). Water flowing from Fish Springs National Wildlife Refuge onto the alkaline flats of the United States Army’s Dugway Proving Ground provides approximately 200 km² of suitable habitat for snowy plovers (Ellis et al. 2014). Blue Lake is located on the Utah Test and Training Range, which is managed by the United States Air Force.

We also collected data along the eastern edge of Great Salt Lake at Saltair and Antelope Island State Park between 2014 and 2017. The Great Salt Lake is the largest saline lake in North America and provides critical habitat to millions of migratory birds (Belovsky et al. 2011). Great Salt Lake hosts one of the largest breeding populations of snowy plovers in North America (approximately 23%; Thomas et al. 2012). Changing shoreline habitat conditions at Great Salt Lake from encroachment of nonnative common reeds (Phragmites australis; Kulmatiski et al. 2010, Long et al. 2017), reduced freshwater inflow (Belovsky et al. 2011, Wurtsbaugh et al. 2017), and large populations of nest predators (Conover 1983, Cavitt et al. 2014) provide multiple challenges to the conservation of snowy plovers and other waterbirds. The eastern edge of Great Salt Lake has experienced rapid human development and urbanization in the last century. Thus, our two study areas represent different levels of human-induced environmental changes with less impacts in western Utah compared to greater impacts at Great Salt Lake.

Locating and monitoring nests

We monitored extant nests and surveyed for new nests at least once per week at each site during the breeding season (early April–mid-August; Paton 1995, Ellis et al. 2015). To estimate the incubation stage of newly located nests, we floated eggs in water and assumed an egg-laying period of 3 d and a 27-d incubation period (Paton 1995, Page et al. 2009). We used Reconyx PC900 infrared-triggered cameras (Reconyx, Holmen, Wisconsin, USA) to determine nest fates and identify predators. Cameras were attached to stakes, placed approximately 2 m away from nests, and were elevated 15–30 cm above the
Fig. 1. Location of study areas in Utah, USA, including the Great Salt Lake (right) and western Utah (Blue Lake top left, Fish Springs National Wildlife Refuge and Dugway Proving Ground bottom left). Black outlines
ground. We set cameras to record two images per second when triggered by a rapid change in temperature within the zone of detection, with no quiet period between triggers. Previous work suggests that cameras do not impact nest survival for snowy plovers (Ellis et al. 2018).

We considered a nest as successful if at least one chick hatched and survived to leave the nest. We identified five groups of predators from photos: (1) gulls (California and ring-billed gulls *Larus californicus* and *Larus delawarensis*, respectively), (2) common raven *Corvus corax*, (3) coyotes, (4) foxes (red foxes at Great Salt Lake sites and kit foxes at western Utah sites) and (5) other (white-tailed antelope ground squirrels *Ammospicillus leucurus*, unidentified mice, Northern Harriers *Circus cyaneus*, and raccoons *Procyon lotor*). We assigned nests as abandoned when adults discontinued incubation of complete clutches. We assigned nests as weather-related failures when nest cups were full of water and adults discontinued incubation or eggs were intact but outside of the nest cup following a weather event. Across our two study areas, we monitored 484 nests with remote cameras and removed only 11 nests from the sample due to camera failure or unclear photos. This resulted in 194 nests from Great Salt Lake and 279 nests from western Utah for analyses of predator-specific nest mortality.

**Measuring nest-site habitat characteristics**

We measured nest-site habitat characteristics once nests had hatched or failed. Vegetation density may influence a predator’s ability to detect a nest via visual or olfactory cues (Martin et al. 2000, Conover 2007). To measure vegetation density surrounding nest cups, we visually estimated the percentage of a Robel pole obscured by cover in four cardinal directions from a distance of 4 m from the nest and a height of 1 m (Robel et al. 1970). We averaged density measurements among the four cardinal directions to obtain a single value for each nest. In addition, we estimated cover surrounding nests by placing a 1-m² frame centered on the nest cup, so that the sides of the frame faced the cardinal directions. We then visually estimated the percentage of bare ground to the nearest 1% over the entire 1-m² area. Snowy plovers often nest in debris or other non-vegetation materials (e.g., cattle dung, carcasses), and thus, we considered only a measurement of bare ground.

**Estimating landscape composition**

We used landscape covers derived from the Southwestern Regional GAP Analysis Project (Lowry et al. 2005) and aerial images (Landsat 7, 2011–2014 and Landsat 8, 2014–2017) to remotely estimate landscape characteristics. Because water levels vary annually at Great Salt Lake (due to variation in annual precipitation and urban water-use; Belovsky et al. 2011) and Fish Springs National Wildlife Refuge (due to differing water-management regimes using an impoundment system), we manually digitized water levels at these study areas from Landsat imagery collected in each year of our study using ArcGIS 10.3 (ESRI 2011). We considered five spatial scales surrounding nests (200, 500, 1000, 2500, and 5000 m buffer sizes) to calculate land cover proportions and density of habitat edges. The five candidate buffer sizes were chosen to allow for comparison of previous nest predation studies (e.g., Boulet et al. 2000, Lyons et al. 2015, Chivacci et al. 2018), and to capture estimated core use areas representing each predator group (Gese et al. 1990, Roth et al. 2004, Kluever and Gese 2017, Ackerman et al. 2018). We chose to use edge density within a buffer as a measure of habitat fragmentation to allow for comparisons among the varying buffer sizes (rather than total edge length). We combined the most abundant land cover types into six classes: (1) grasses (invasive annual grasses, semi-desert grassland), (2) open water, (3) playa, (4) shrubs (big sagebrush shrubland, semi-desert shrub steppe, mixed salt desert scrub, greasewood flat), (5) emergent marsh, and (6) human development (impervious surfaces accounted for 20–100% of total cover; Lowry et al. 2005). Nests located near human development were relatively rare, and thus, we
did not have enough samples to separate intensity of human development. We used the raster (Hijmans 2019) and sp (Pebersa and Bivand 2005, Bivand et al. 2013) packages in R (R Development Core Team 2018) to create varying buffers around nests and calculate land cover proportions and density of habitat edges within each buffer size. In addition, for each nest we calculated the distance to the nearest nest on each day of the breeding season to be included as a time-varying covariate using the geosphere package in R (Hijmans 2017).

Analysis

We used a cause-specific hazard model in a Bayesian framework to examine multiple sources of nest mortality (Heisey and Patterson 2006, Heisey et al. 2007). Nest exposure days began the day the camera was placed at the nest resulting in a sample size of 4874 nest exposure days. We right-censored abandoned and flooded nests \( (n = 10) \) because we were primarily interested in dynamics of nest predation. The model has the form

\[
y_i \sim \text{Multinomial}(S, P_j = 1, \ldots, P_J = 1) \tag{1}
\]

\[
S = e^{-\sum_{j=1}^{J} h_j / P_j} = (1 - S) \left( \frac{h_j}{\sum_{j=1}^{J} h_j} \right),
\]

where \( y_i \) are the observed nest fates of nest \( i \) on each exposure day that included surviving \( (S) \), the exposure day and failing \( (P_j) \) from one of \( J \) causes of predation (foxes \([ f] \), coyotes \([ c] \), gulls \([ g] \), ravens \([ r] \), and other \([ o] \)), and the 1 indicates a single trial per day. The \( h_j \) are time-averaged mortality hazard rates of predator \( j \) at daily intervals (Ergon et al. 2018), which closely approximates a continuous time hazard model while acknowledging the discrete nature of our data (Heisey and Patterson 2006, Heisey et al. 2007).

**Multiscale nest mortality model.**—We incorporated five candidate scales for the predictors of landscape characteristics \( X \) (land cover proportions and density of habitat edges) using Bayesian latent indicator scale selection (Stuber et al. 2017). We modeled the scale of each predictor as a latent multivariate indicator variable \( \text{sc}_j \), representing a matrix of seven landscape covariates at five spatial scales for each cause of nest predation \( j \). This indicator variable produced posterior distributions that essentially weight the candidate scales for each landscape predictor. The effect of each landscape predictor was moreover estimated by a regression coefficient which was weighted among spatial scales during the MCMC process and contained within the matrix of coefficients for cause of nest predation \( j \beta_j \). Although weighted regression coefficients do not provide individual estimates for effects of landscape covariates at every spatial scale, we felt this approach was warranted given the number of individual models that would be required to evaluate effects of seven landscape covariates, at five spatial scales, for four predator groups. In addition, this multiscale approach avoids the issue of collinearity among the different scales because only one scale of each predictor is included in any given MCMC iteration (Stuber et al. 2017). We incorporated additional predictors in \( Z^{fi} \), including the study area that nest \( i \) was in (Great Salt Lake or western Utah), nearest neighboring nest at time \( t \) (an index of density dependence), percent bare ground at the nest \( i \), and vegetation density at nest \( i \) with associated coefficients represented by \( \alpha_i \). The effects of these predictors on predator-specific hazard rates were collectively modeled through a log-link as:

\[
\log(h_i^{J}\gamma_t) = X^{t} \beta^{fi} [\text{sc}_j] + Z^{fi} \alpha_j + \varepsilon_j^{fi} + \gamma_j^{fi}
\]

\[
\varepsilon_j^{fi} \sim \text{Norm}(0, \sigma_j^{2,fi}), \gamma_j^{fi} \sim \text{Norm}(0, \sigma_j^{2,fi})
\]

where year \( r \), and day of season \( t \) were included as random effects \( (\varepsilon_j^{fi} \text{ and } \gamma_j^{fi} \text{, respectively}) \) to account for temporal variation in nest predation, which were each modeled using a normal distribution on the link scale with a mean of zero and variance \( \sigma_j^{2,fi} \) or \( \sigma_j^{2,fi} \), respectively.ests that were depredated by predators in the other category were modeled as an intercept-only with no covariates or random effects because there were relatively few observations in this category. Nest predation by gulls occurred only at Great Salt Lake, so we did not estimate the effect of study area for this cause of failure. All continuous predictors were scaled to have a mean of zero and standard deviation of one.

**Priors and estimation.**—We chose vague priors for all parameters, including a uniform \([0, 10]\) distribution for hyperpriors on the standard deviation for random effects, and a normal distribution with mean 0 and standard deviation of 10 for the
coefficients $\beta_j$ and $\alpha_j$. We used a categorical distribution for indicators of the candidate scales $s_c$, with equal prior probabilities that summed to 1 (because we had five candidate scales, each scale had a non-informative prior weight of 0.20). Parameters in the nest mortality model were estimated using a Bayesian application of MCMC sampling (Gelfand and Smith 1990), implemented in JAGS 4.3.0 (Plummer 2017) and cast in R via the package jagsUI (Kellner 2018; R code is provided in Appendix S1). We generated 3 MCMC chains for 200,000 iterations with 50,000 burn-in and 50,000 adaptive iterations, and a thinning rate of 50. We assessed convergence using the Gelman-Rubin diagnostic $R$ (Gelman et al. 2004) and visual inspection of trace plots. Convergence was achieved for estimated parameters (all $R < 1.1$, with trace plots showing mixing among stationary MCMC chains).

**Results**

Mean nest success (across a 27-day incubation period) in an average year was almost 2 times higher in western Utah (0.71, 95% Bayesian Credible Interval [BCI] = 0.62–0.80) than at Great Salt Lake (0.39, 95% BCI = 0.25–0.56). Gulls and ravens were dominant nest predators at the Great Salt Lake with mean daily hazard rates across the breeding season: 0.06 (95% BCI = 0.01–0.11) and 0.05 (95% BCI = 0.01–0.016), respectively, compared to 0.006 (95% BCI = 0.002–0.01) for foxes and 0.005 (95% BCI = 0.002–0.01) for coyotes. Conversely in western Utah, coyotes, foxes, and ravens had relatively similar daily hazard rates: 0.03 (95% BCI = 0.002–0.08), 0.04 (95% BCI = 0.002–0.10), and 0.03 (95% BCI = 0.002–0.07), respectively. The residual yearly variation in nest mortality probabilities was greatest for gulls (SD on the link scale = 0.84, 95% BCI = 0.02–4.53), compared to 0.43 (95% BCI = 0.02–1.43) for ravens, 0.31 (95% BCI = 0.01–1.07) for coyotes, and 0.31 (95% BCI = 0.01–1.05) for foxes. Most nests were directly located in the playa land cover type ($n = 449$), with the remaining located in human developed ($n = 5$), marsh ($n = 14$), and grass ($n = 5$) areas, but all land cover types were represented at both study areas within buffers surrounding nests. At the nest site, the mean (± SE, range) proportion of bare ground surrounding nests was 0.55 (± 0.01, 0.00–1.00) and the mean height of vegetation covering the Robel pole was 21.00 cm (± 4.67, 0.00–46.66). The mean distance to the nearest active nest was 348.72 m (± 17.78, 3.52–1695.91).

**Scale selection of landscape characteristics**

Using Bayesian latent indicator scale selection, we did not identify a common spatial scale that best predicted the influence of landscape characteristics on nest predation among predators (Fig. 2). Further, the spatial scale at which landscape characteristics influenced nest predation within predator species often varied with land cover categories. However, the proportion of playa was consistently estimated to predict nest predation at large spatial scales (2500 and 5000 m) for all predator groups (2500 m posterior probability: 0.64, 0.73, 0.57, and 0.61 for ravens, gulls, coyotes, and foxes, respectively). Similarly, the density of habitat edges was estimated to predict nest predation at large spatial scales for ravens (2500 m posterior probability: 0.56; 5000 m posterior probability: 0.41), gulls (2500 m posterior probability: 0.63), and coyotes (2500 m posterior probability: 0.42; 5000 m posterior probability: 0.55), but probabilities for foxes were less discriminated among spatial scales (2500 m posterior probability: 0.44; 1000 m posterior probability: 0.27).

The influence of proportions of grass, marsh, and shrub on nest predation by foxes was most supported at a 500 m scale (posterior probabilities: 0.53, 0.64, and 0.57, respectively), whereas the influence of grass and shrub on nest predation by coyotes was most supported at larger spatial scales (grass 2500 m posterior probability: 0.48; grass 5000 m posterior probability: 0.34; shrub 2500 m posterior probability: 0.58; shrub 1000 m posterior probability: 0.27). The influence of human development on nest predation by coyotes was not clearly supported at a single spatial scale; however, development influenced predation by gulls at smaller spatial scales (200 m posterior probability: 0.73) and larger scales for ravens and foxes (2500 m posterior probabilities: 0.60 and 0.55, respectively). The proportion of water most influenced nest predation by gulls at 500 m (posterior probability: 0.70) but was not clearly supported at any spatial scale for coyotes, foxes, and ravens.
Effects of landscape and nest-site characteristics on nest predation

Based on the posterior distributions of slope parameters, nest mortality hazard rates by all predators decreased with proportions of playa and marsh surrounding nests (90% of posteriors < 0, Fig. 3), with the exception of the effect of playa on nest predation by foxes (64% of $\beta_{\text{playa}}^{f}$ posterior was <0). In addition, predation from all predators exhibited positive relationships with the density of habitat edges, suggesting a negative edge effect on snowy plover nest survival, though there was less support for foxes and ravens (71% of $\beta_{\text{edge}}^{f}$ > 0, 72% of $\beta_{\text{edge}}^{r}$ > 0). The remaining land cover types elicited variable responses by nest predators. Nest predation increased with the proportion of grass for foxes (96% of $\beta_{\text{grass}}^{f}$ > 0), yet decreased for ravens, gulls, and coyotes (64% of $\beta_{\text{grass}}^{r}$ < 0, 100% of $\beta_{\text{grass}}^{g}$ < 0). Nest predation by foxes, coyotes, and ravens increased with proportion of shrubs and decreased for gulls (90% of posterior distributions on the same side of 0 as the mean). Open water and human development increased nest predation by gulls (90% of posterior distributions >0), while human development decreased the probability of nest predation by foxes (97% of $\beta_{\text{devel}}^{f}$ < 0). Human development and open water were not influential on nest predation by coyotes and ravens as indicated by wide posterior distributions and means centered near 0 (Fig. 3).

At the nest site, predation by gulls increased with percent bare ground and decreased with...
vegetation density, whereas nest predation by ravens and foxes increased with vegetation density (90% of posterior distributions on the same side of 0 as the mean, Table 1). Nest predation by ravens and foxes decreased as distance to nearest nest increased (90% of posterior distributions $< 0$, Table 1, Fig. 4). We did not detect effects of nest-site variables on nest predation by coyotes as indicated by wide posterior distributions and means centered near 0 (Table 1).

**DISCUSSION**

Patterns of predation can be influenced by landscape structure, and thus, understanding these patterns can provide useful tools for managing populations that are limited by predation. We found that relationships between nest predation by specific predators and landscape characteristics were not supported at a single spatial scale, indicating that multiscale approaches may be appropriate when assessing the influence of habitat landscapes on nest predation by multiple species. Foxes and ravens are important nest predators for many ground-nesting species (Draycott et al. 2008, Liebezeit and Zack 2008, Peterson and Colwell 2014, O’Neil et al. 2018, Ellis et al. 2020), yet were influenced by the landscape at different spatial scales. In addition, relationships between land cover...
characteristics and nest predation by mammalian predators were more supported at larger spatial scales for coyotes compared to smaller spatial scales for foxes, which was consistent with our prediction of differing responses to the landscape based on body size (Gehring and Swihart 2003). Within predator groups, the most supported spatial scales often varied depending on the landscape characteristic, suggesting that there may be a hierarchy of how landscape features influenced predator habitat use when preying upon nest. For example, nest predation by ravens was influenced by the density of habitat edges, human development, and playa at 2500 and 5000 m scales, yet was strongly influenced by marsh at 200 m. This overall variation in predator responses to the landscape may compromise the effectiveness of management strategies that attempt to increase avian productivity by altering or restoring habitats when based on habitat relationships at a single spatial scale.

Although our results indicated variation among predator species in their responses to landscape characteristics, general patterns emerged regarding proportions of playa and marsh, and the density of habitat edges. Nest predation by all predators decreased with the proportion of playa surrounding nests and this relationship was supported at large spatial scales. While we predicted that nest predation by mammalian predators would increase with the density of habitat edges, we detected a positive relationship for all predator species. The influence of habitat edges on nest predation often varies with the predator community (Lahti 2001) and can be a dynamic process through time (Malzer and Helm 2015). Studies of this effect, however, have largely focused on agricultural landscapes with hard edges (Lahti 2001, Batary and Baldi 2004, Stephens et al. 2004), while studies from lower-contrast edges, such as the transition from marsh to playa, are less common (Suvorov et al. 2014, Malzer and Helm 2015). In our study, the influence of edge density on coyote nest predation had the highest posterior probability at 5000 m, which could indicate that the actual scale of this effect is larger than what we measured (Jackson and Fahrig 2015). Yet
taken in combination, our results suggest that large, unfragmented playa habitats are important to snowy plover nesting success, when similar nest predators are present. In addition, nest predation by all predators decreased with the proportion of marsh, although this relationship was not supported at consistent spatial scales. Marshes support a diversity of species during the breeding season which may reduce predation pressure on birds nesting in nearby playa habitats by providing alternative food resources for nest predators (Spautz et al. 2006, Tozer et al. 2010, Laidlaw et al. 2015). Wetland habitats are among the most endangered ecosystems worldwide but provision more ecosystem services per unit area than any other type of ecosystem (Dodds et al. 2008), and wetlands within the Great Basin of North America are continuing to degrade due to reduced water levels (Wurtsbaugh et al. 2017, Sennet et al. 2018, Haig et al. 2019). Our study provides additional support for the importance of conserving large wetland complexes (of both playa and marsh habitats) for the reproductive success of avian species using these habitats (Smart et al. 2006, Kentie et al. 2013, Rannap et al. 2017).

The Great Salt Lake was dominated by avian predators, and ravens are often associated with anthropogenic subsidies and water sources (Boorman et al. 2006, Kristian III and Boorman 2007); thus, it is unclear why we did not detect an effect of human development on nest predation by ravens. In addition, the Great Salt Lake hosts some of the largest colonies of California and ring-billed gulls in the interior west of North America with many colonies centered around landfills and human developments (Conover 1983, Cavitt et al. 2014). Gull predation can have substantial effects on seabird colonies (Scopel and Diamond 2017), yet have not been implicated as important shorebird nest predators (but may be an atypical occurrence when nests are near a large gull colony; Page et al. 1983). Gulls have had little effect on survival of Arctic shorebird nests (Smith et al. 2007, Liebezeit and Zack 2008, McKinnon and Béty 2009, Saalfeld et al. 2013), particularly when colonies are near landfills likely because organic waste is easier to find than shorebird nests (Saalfeld et al. 2013). Further, close proximity to gull colonies may have positive effects on shorebird nest survival when gulls act as a protector (Swift et al. 2018). However, gulls may have substantial effects on shorebird chick survival, which we did not measure (Weiser and Powell 2011, Swift et al. 2018). Further understanding of gull diets and landfill management (e.g., timing and location of organic waste deposits) could lead to strategies which decrease the impacts of gull predation on shorebird reproduction when large gull colonies are adjacent (Weiser and Powell 2011, Saalfeld et al. 2013, Ackerman et al. 2018).

Mammalian meso-predators may also alter their space use around human developments with species- and individual-level variation in the direction of responses (Atwood et al. 2004, Fischer et al. 2012, Newsome et al. 2015). One relevant example includes meso-predator use of roads or levees as movement corridors into wetland environments (Frey and Conover 2006), and nest proximity to gravel roads has been shown to be negatively related to snowy plover nest success (Ellis et al. 2015). Our results alternatively suggested that nest predation by foxes decreased with proportions of human development, and nest predation by coyotes was not influenced by human development. Although both kit foxes and red foxes occupy habitats near urban developments (Kozlowski et al. 2008, Gehrt et al. 2010), foxes may have avoided developments when preying upon nests, potentially due to an overall scarcity of protective cover in snowy plover nesting areas. Because of the rarity of nest predation events by red foxes at the Great Salt Lake, we did not test species-specific patterns of nest predation by foxes, and additional data could provide insights into how red foxes and kit foxes differ in their habitat use when preying upon nests. Nest predation did increase with the proportion of shrub (by foxes and coyotes), and proportion of grass (by foxes), suggesting that mammalian nest predators use these respective land cover types to move into areas used by snowy plovers for nesting. Kit foxes and coyotes in western Utah have overlapping distributions; however, kit fox space use has been shown to correspond with an avoidance of coyotes rather than access to prey (Kozlowski et al. 2012). Because of this spatial avoidance among meso-predators, kit foxes use extreme environments with limited food resources, such as playa and bare mud flats, more often than coyotes (Kozlowski et al. 2008, Lonsinger et al. 2017).
In addition to landscape characteristics influencing nest predation, we found that the spatial configuration of nests influenced nest predation by foxes and ravens (nest predation decreased with nest dispersion), but not gulls and coyotes. Many bird species breed in aggregated patterns, where conspecifics nest nearer than expected by random chance, and seemingly suitable habitat may remain unoccupied (Stamps 1988, Brown and Brown 2001). The degree of aggregation may depend on the size or quality of nesting areas (Melles et al. 2009), population density (Patrick and Colwell 2018), or behavioral decisions based on successful breeding by conspecifics (Rioux et al. 2011). Snowy plovers nest in loose aggregations but the average distance between nests varies among populations (e.g., 144 m in Texas compared to 1841 m in northern California; Saalfeld et al. 2012, Patrick and Colwell 2018). In our study, 40% of successful nests were within 200 m of another nest when it finished, compared to 63% of nests depredated by either foxes or ravens. These findings complement previous work which found that foxes and ravens have low consumption rates of nests when nest abundance is low, but this rate increases with nest abundance until eventual satiation is reached (Ellis et al. 2020). Our results suggest that the maintenance of low nesting density may be a useful antipredator adaptation when certain predators develop a search image for nests, and conservation of large unfragmented landscapes allows for this (Page et al. 1983).

Studies investigating the effects of vegetation structure at the nest site on nest fate in shorebirds have often found conflicting patterns where higher nest success may be related to little to no cover (e.g., Colwell et al. 2011), or alternatively related to some vegetation cover (e.g., Swaisgood et al. 2018). An often-cited explanation for the lack of consistent patterns is that the local predator community may be related to the importance of vegetation cover on nest fate (Swaisgood et al. 2018). While we predicted that characteristics at the nest site would influence nest predation by avian predators because of their reliance on visual stimuli for foraging (Schmidt 1999), we detected a response to vegetation structure by gulls but not ravens. Thus, an understanding of the nest predator community will better inform conservation strategies that attempt to create attractive nesting habitats, such as engineered gravel patches or sandbars, and reduce the likelihood of an ecological trap (Katayama et al. 2010, Ellis et al. 2015, Hunt et al. 2018). We speculate that at the nest-site scale, predators are also influenced by adult incubation behaviors (Smith et al. 2012), and olfactory cues (Conover 2007), which we did not assess.

Given that studies of nest predation are often intended to directly inform management and conservation strategies, it is important to assess how different species of nest predator respond to habitat characteristics at varying spatial scales. Our results support recommendations to evaluate species-specific patterns of nest predation at multiple landscape scales (Chiavacci et al. 2018). Rather than assigning a single best scale to assess complex ecological processes (Stuber and Fontaine 2019), our approach using weighted beta coefficients allows habitat managers to consider many spatial scales when multiple nest predators are present to design more effective management plans. Our results suggested that nest predation decreased with proportions of playa and marsh at large spatial scales, indicating that large-scale restorations of these habitats should be favored over small ones. Shorebirds breeding within our study areas may therefore benefit from the maintenance of large, unfragmented wetland areas, rather than smaller, disjoint wetlands when future human developments or landscape alterations are being considered.

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DATA AVAILABILITY

Nesting data are available on Zenodo https://doi.org/10.5281/zenodo.3594125.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ec2.3257/full