DISSERTATION

EFFECTS OF PREDATOR STRATEGIES ON THE NESTING ECOLOGY OF SNOWY PLOVERS (*Charadrius nivosus*)

Submitted by

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ABSTRACT

EFFECTS OF PREDATOR STRATEGIES ON THE NESTING ECOLOGY OF SNOWY PLOVERS (*Charadrius nivosus*)

Predation on nests has been identified as the primary source of reproductive failure for a wide range of avian species and across a diversity of habitats. During the nesting period, individuals are bound to a particular location, thus it is not surprising that nest predation is a strong evolutionary force and should lead to nest sites, breeding behaviors, and life-history traits that reduce its negative effects. Yet as human-induced environmental change rapidly progresses, historic predator-prey interactions may also be altered. Understanding predictors of nest predation will become increasingly complex as species distributions and behaviors shift in conjunction with other environmental stressors. Consequently, clarifying how anthropogenic changes affect nest predation first depends on understanding predator ecology. Little information exists on the foraging behaviors of specific nest predators and mechanisms of locating nests. Nests may be susceptible to predation by multiple predators each having a different relative importance depending on patterns of habitat use, nest density, and interspecific interactions. Thus, identifying nest predators is a necessary first step to a more holistic assessment of drivers of variation and mechanisms of nest predation.

Snowy plovers (*Charadrius nivosus*) are small, ground-nesting birds that occupy coastal beaches and sparsely-vegetated playa wetlands. This species is one of the rarest shorebirds in North America with approximately 26,000 individuals, despite a broad distribution. Dependence on shorelines has made snowy plovers vulnerable to habitat loss and human disturbance. Snowy

plovers are moreover a species of conservation concern throughout North America and the Pacific coast population is listed as threatened under the U.S. Endangered Species Act. Like many avian species in peril, increased nest predation has been identified as a primary factor limiting population recovery. Snowy plovers cope with high rates of nest failure by laying multiple clutches during the breeding season whether the first nest was successful or not. Both sexes incubate nests and pair monogamously, however, snowy plovers display an unusual pattern of facultative polyandry in some populations once chicks hatch. Male adults tend chicks and lead them to foraging areas while females often desert the brood to search for additional mates, which allows for their multi-clutching strategy in seasonal environments. Despite more than 20 years of intensive research on snowy plovers because of their conservation status, significant gaps remain that limit our understanding of the role that specific predators play in shaping nest mortality and snowy plover behavioral responses to their different foraging strategies.

We sought to improve our understanding of variation in predator-specific nest mortality and the influence of risks of nest predation by specific predators on parental care. First, we investigated the accuracy of traditional field methods (using eggshell evidence at nests) in determining nest fate, and identified sources of variation in accuracy. We discuss situations where traditional field methods for assigning nest fate may lead to inaccuracies. In addition, we compared nest survival rates from a sample of nests monitored with remote cameras to those monitored with traditional field methods to address concerns that remote cameras may influence predator abilities in locating nests. We did not detect an effect of remote cameras on snowy plover nest survival, which allowed us to further evaluate patterns of predator-specific nest mortality without this concern.

Next, we investigated how nest abundance influenced the effects of multiple competing predators on nest mortality. The functional relationship between the consumption rate of prey and prey abundance is an important component of predator-prey dynamics. However, these ‘functional responses’ are more difficult to predict when multiple predators compete for a shared prey. Within a Bayesian framework, we modeled predator-specific hazard rates for nest mortality while combining a functional response analysis. The flexibility of this approach allowed us to incorporate statistical uncertainty around estimates of nest abundance that were used as predictor variables. Species of nest predators differed in their response to nest abundance, and patterns were not common among types of predators (avian or mammalian). Further, predator-specific hazards were often not independent throughout the breeding season suggesting that various forms of competition and interspecific interactions may occur between nest predators.

Habitat features surrounding the locality of nests can have varying consequences for nest survival. For snowy plovers, and other ground-nesting species that nest in open habitats, avoidance of nest predation is generally achieved through eggshell camouflage and distraction displays by incubating adults. However, variation in nest survival often cannot be explained by nest-site characteristics alone and may be better explained by considering multiple scales of the landscape, because large-scale features influence the numerical abundance and foraging patterns of nest predators. We evaluated several potential landscape drivers of predator-specific nest mortality and identified proportions of playa and marsh habitats (at large spatial scales) surrounding nests as having the strongest influence on nest predation by all predator species. The importance of large patches of wetland habitats for nest survival indicate that restoration programs in the future should prioritize larger, continuous wetlands over small, fragmented wetlands. In addition, these results suggest that nesting in playa habitats may be an adaptive strategy for avoiding common nest predators.

Finally, we used the aforementioned predator-specific hazard rates of nest mortality to represent risks of nest predation, and examined whether breeding pairs altered incubation behaviors in response to these risks. One benefit to this approach compared to using predator density as an indication of risks of nest predation is that hazard rates varied daily and with nest-specific habitat characteristics for each predator species, and therefore indexed the realized risk of predation for each nest on each day. Our results indicated that breeding pairs increased parental care when risks of nest predation by foxes (*Vulpes* spp.) and gulls (*Larus* spp.) increased, but this relationship was not consistent for all predator species. In addition, breeding pairs did not exhibit the same amount of behavioral plasticity in response to risks of nest predation, suggesting that differences in ‘personality’ of breeding pairs or adult state (age or body condition) may contribute to the amount of plasticity in parental care that is exhibited.

In summary, this dissertation provides valuable information for researchers and managers interested in the dynamics of nest predation. More broadly, our approach in Chapter 2 provides a flexible example of evaluating predator-prey dynamics in the presence of competing predators. We have shown that remote cameras can be a valuable tool for monitoring nests, identifying nest predators, and quantifying incubation behaviors without detrimental effects on nest survival. Our results revealed non-independence in nest predation among competing predators, which has considerable implications for many management and conservation strategies that attempt to increase avian productivity by removing certain predator species. We have also shown that nest predators responded to the landscape at different spatial scales, which could limit the effectiveness of habitat management when based on a single spatial scale. We have presented evidence that incubating birds can perceive and respond to risks of nest predation in a natural system, providing insight into the evolution of parental care in variable environments. The continued expansion of common nest predators (e.g., corvids and mammalian meso-predators) because of their use of anthropogenic subsidies makes our work relevant to researchers and managers of other avian species nesting in wetland habitats.

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SUMMARY

Nest survival is a key demographic parameter, yet little effort has been made to improve the accuracy of field-based methods for assigning nest fates to shorebird nests. We used remote cameras to validate estimates of nest fate from field methods and to assess variation in accuracy of nest-fate assignment for Snowy Plover *Charadrius nivosus* in Utah, USA. We correctly identified the fates of 84% of nests in the field and photos from camera monitoring revealed incorrect assignments for 22% of successful nests and 7% of depredated nests. Traditional field methods could be improved by checking nests more frequently when hatching date nears and spending additional time searching for eggshell evidence, especially when nests are in areas susceptible to weather disturbance.

INTRODUCTION

Nest survival is a key demographic parameter for understanding avian productivity and population dynamics. Incorrect assignments of nest fate may have implications for population modelling (Ball and Bayne 2012) and diminish the efficacy of management strategies based on demographic data. Estimation and modelling of nest survival have received considerable attention (Jones and Geupel 2007), however only limited efforts have been made to validate assignments of nest fate based on field observations. Correct assignment of nest fates is

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important because nest survival estimators constitute a special class of ‘known-fate’ survival estimators where the fates of uncensored nests are treated as ‘known’, but the timing of failure is not necessarily known (failure often occurs between nest visits) (Rotella et al. 2009). Many species of shorebirds remove eggshells from nest cups and chicks leave nests shortly after hatching (Mabee et al. 2006). Current methods using evidence at nests to determine shorebird nest fate may be incorrect because the final nest visit is often to an empty nest with no sign of adults or young in the area. In these cases, nest fate is generally determined by eggshell evidence at the nest and nest age (Page et al. 1985; Paton 1995; Mabee 1997; Mabee et al. 2006; Smith et al. 2007).

Remote cameras provide a reliable method for monitoring nests (Cutler and Swann 1999; Bolton et al. 2007). Remote cameras have been used to monitor shorebird nests, examine incubation behaviours (Smith et al. 2012; Burns et al. 2013), and identify nest predators (Bolton et al. 2007; Liebezeit and Zack 2008; Demers and Robinson-Nilsen 2012). Although remote cameras can help monitor shorebird nests, the effects of camera presence on nest survival could be negative if predators are attracted to a novel stimulus. Alternatively, camera-monitoring may result in higher rates of nest survival if researcher disturbance is minimized or predators avoid unfamiliar features.

To better understand factors influencing the correct assignment of nest-fate in the field, we monitored Snowy Plover *Charadrius nivosus* nests using infrared-triggered cameras and independently assigned nest fates using traditional field observations. Snowy Plovers are a species of conservation concern throughout much of their range (e.g. the Pacific population is listed as threatened under the U.S. Endangered Species Act) (USFWS 2012). Because of their conservation status, many populations of Snowy Plover are heavily monitored making the validation of field methods particularly important. Our objectives were to: 1) assess the accuracy of nest-fate assignment from field methods and identify factors influencing error; and 2) determine whether camera monitoring influenced daily survival rate. We predicted that the fate of successful nests would be more ambiguous than unsuccessful nests because chicks are precocial and do not remain in the nest and adults will remove eggshells after hatching.

METHODS

Study Areas

We monitored nests of Snowy Plover in two regions of Utah, USA between 2011 and 2016. These regions included 1) Great Salt Lake (Saltair [40°46’00” N, 112°09’50” W] and Antelope Island State Park [41°05’08” N, 112°08’08” W], 2014–2016), and 2) western Utah (Fish Springs National Wildlife Refuge and the southwest corner of the United States Army Dugway Proving Ground [39°55’40” N, 113°24’50” W; 2011–2016] and Blue Lake [40°32’00” N, 114°01’08” W; 2016]). Great Salt Lake hosts the largest breeding population of Snowy Plovers in North America (23% of approximately 26,000) (Thomas et al. 2012) whereas populations in western Utah are relatively small and tied to limited water sources (Ellis et al. 2014).

Field Procedures

We conducted nest surveys at least once per week to locate new nests and monitor extant nests at each site. Once located, we floated eggs to estimate nest age and initiation date assuming an egg-laying period of 3 days and a 27-day incubation period (Paton 1995; Page et al. 2009). We recorded nest substrate by noting the location of the nest in either vegetation, bare ground, or on or next to debris. We chose nests for camera monitoring based on age of nests (≥ four days after the onset of incubation to minimize risk of abandonment) and camera availability. We used Reconyx PC900 infrared-triggered cameras (Reconyx, Inc., Holmen, Wisconsin) to monitor nests. We mounted each camera to a stake and positioned it 15 cm above the ground and approximately 2 m from the nest. Cameras were set 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.

Once nests had finished, we recorded descriptions of remains including condition of nest cup and surrounding area, eggshell fragments, and condition of eggshell membranes (missing, or intact). We sorted through the nesting substrate in the field to identify small eggshell fragments. We assumed signs of successful nests included small eggshell fragments (1–5 mm; produced during pipping) inside the nest cup, eggshell membrane partially or completely separated from eggshell, eggshell tops or bottoms, and chicks in the nest cup (Mabee 1997; Mabee and Estelle 2000; Mabee et al. 2006). We considered a nest as successful if at least one chick hatched and survived to leave the nest. Evidence of depredated nests included eggs disappearing prior to the expected date of hatching or presence of yolk or large eggshell fragments (≥ 6 mm). We analysed images from cameras to determine nest fate after descriptions of nest remains had been recorded in the field and nest fate had been assigned based on these descriptions.

Data Analyses

We assessed the accuracy of nest fate assignment by comparing the proportion of successful and depredated nests assigned in the field to those quantified from photos using two-tailed Fisher exact tests. To determine factors influencing the correct assignment of nest fate, we used logistic regression with the correct assignment of fate based on comparison of camera photos to field assignment as the response variable (1 was correct, 0 was incorrect). We examined whether incorrect assignments were influenced by the individual observer, attributes of the nest (nest age and nesting substrate), and nest predator. Specific covariates included: predator, nest age, observer (*n* = 5), nesting substrate, and number of days between actual finish date and date checked by observers. We standardised nest age (z-score) to allow for comparison across studies. We identified five groups of predators from photos: 1) gulls *Larus* spp. (*n* = 49), 2) Common Raven *Corvus corax* (*n* = 39), 3) Coyotes *Canis latrans* (*n* = 21), 4) foxes (Red Fox *Vulpes vulpes* at Great Salt Lake sites and Kit Fox *Vulpes macrotis* at western Utah sites; *n* = 31) and 5) small mammals (White-tailed Antelope Ground Squirrel *Ammospermophilus leucurus* and unidentified mice; *n* = 9). Thus, the covariate for predator represented five predator types with successful nests as a reference. We assigned nests as abandoned when adults discontinued incubation of complete clutches. We assigned nests as weather-related failures when there was evidence of flooding in the nest cup or eggs were intact but outside of the nest cup following a weather event. We did not incorporate nests that were abandoned (*n* = 6) or failed due to weather (*n* = 7) into the analysis because our accuracy in assignment of these fates was 100%.

Because we had relatively few instances where nest fate was incorrectly assigned, we limited our models to a maximum of two main effects to avoid overfitting. Considering only two-variable models may have limited our ability to predict inaccuracies in nest-fate assignment, however this approach helps to avoid spurious effects from fitting models with too many parameters relative to the sample size (Burnham and Anderson 2002). To avoid fitting models with collinear predictors, we assessed correlation coefficients between pairs of predictor variables and none exceeded $|0.5|$ (Pearson correlation). We considered all combinations of covariates resulting in 16 *a-priori* models including 5 univariate models, 10 two-variable models, and an intercept-only model. We also calculated the Variance Inflation Factor (VIF) for each model considering a threshold value of three (Zuur et al. 2010). We used Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002) to compare support among models. All analyses were conducted in R (version 3.3.1; R Development Core Team, 2012). Using Akaike model weights, we averaged models using the MuMIn package (Barton 2016) in R. Because evidence at the nest is dependent on nest fate (i.e. small fragments indicate successful nests and would be correctly assigned in the field but may also lead to an incorrect assignment of successful when nests were depredated), we used Fisher's exact tests (with Bonferroni correction) to compare evidence at nests between correct and incorrect field assignment.

To test whether camera-monitoring influenced nest predation, we estimated daily survival rates between nests monitored with cameras and an additional set of nests monitored without cameras during the same time and at the same study sites (Table 1-1). We estimated daily survival rates using the nest survival model in the RMark package (Dinsmore and Dinsmore 2007; Laake and Rexstad 2012) in R. Exposure days began the day the nest was found (for nests monitored without cameras) or the day the camera was placed at the nest (for camera-monitored nests). This method provides a conservative estimate of daily survival rate for nests monitored with cameras (McKinnon and Bêty 2009). Estimates of daily nest survival were derived from a single model which included presence of cameras in addition to effects of site, year, and nest age, which have been shown to contribute to variation in daily nest survival (Ellis et al. 2015). To evaluate parameter significance, we assessed the degree of overlap in 95% confidence intervals around zero for beta estimates. We calculated estimates of nest success by exponentiation of daily survival rate to 27, consistent with a 27-day incubation period with confidence intervals calculated using the delta method (Seber 1986).

RESULTS

We monitored 358 Snowy Plover nests with infrared-triggered cameras between 2011 and 2016. We removed 17 nests from our sample due to camera error (*n* = 3), unhatched eggs (*n* = 1), abandonment (*n* = 6), and weather-related failure (*n* = 7). Mean number of days between actual finish date and last date checked was 4.19 (± 0.10 se) days. We correctly identified the fates of 287 (84%) nests in the field. Photos from camera monitoring revealed incorrect assignment for 44 of 197 (22%) successful nests and 10 of 144 (7%) depredated nests. Overall, the odds of correctly assigning the fates of depredated nests were 3.84 (95% confidence interval (CI) = 1.82–8.90; $P < 0.01$) times greater than the odds of correctly assigning the fates of successful nests.

All models had VIF values < 3, and therefore we considered each additive, two-variable combination as plausible. Our most supported model ($w_i = 0.51$) included nest outcome separated by predator type (with successful nests as a reference) and nest age (Table 1-2). Assignment of nest fate (successful or depredated) in the field was less likely to be correct as nest age increased ($\beta = -0.66$, 95% CI = -1.33–-0.07). Nests depredated by Coyotes ($\beta = 1.11$; 95% CI = -0.59–4.03), foxes ($\beta = 1.55$; 95% CI = -0.12–4.48), gulls ($\beta = 1.05$; 95% CI = -0.31–2.95), and Common Ravens ($\beta = 1.20$; 95% CI = -0.10–3.06), were positively related to correct assignments of nest fate compared to successful nests, though confidence intervals overlapped zero in each case. However, nests depredated by small mammals were less likely to be correctly assigned than successful nests ($\beta = -1.68$; 95% CI = -1.33–-0.07; Fig. 1-1a). Our second competing model ($w_i = 0.19$) included predator and an effect of nesting substrate. Nests that were located on vegetated substrates were more likely to be correctly assigned a nest fate than nests located on barren substrates ($\beta = 1.02$, 95% CI = 0.12–1.89).

From model-averaged estimates, the probability (± 95% CI) of correctly assigning nest fate depredated by small mammals was 0.55 (0.16–0.95) compared to 0.94 (0.82–1.00) for Coyotes, 0.95 (0.86–1.00) for foxes, 0.94 (0.85–1.00) for gulls, 0.94 (0.85–1.00) for Common Ravens, and 0.82 (0.74–0.90) for successful nests (Fig. 1-1a). The odds of incorrectly assigning a depredated nest as successful were 210.48:1 (95% CI = 25.24–3556.65; $P < 0.01$) when small fragments were present. Alternatively, the odds of incorrectly assigning a successful nest as depredated were 27.63:1 (95% CI = 5.75–264.53; $P < 0.01$) when there were egg pieces present and 62.55:1 (95% CI = 18.77–276.72; $P < 0.01$) when there was no evidence at the nest (Fig. 1-1b).

We constructed valid encounter histories for 508 nests over a 109-day monitoring period for nest survival analysis (29 April to 16 August; Table 1-1). We did not detect a significant effect of camera-monitoring on daily nest survival ($\beta = 0.12$, 95% CI = -0.19–0.43; Fig. 1-2). Overall nest success for nests monitored with cameras was 0.46 (95% CI = 0.38–0.53) compared to 0.42 (95% CI = 0.31–0.51) for nests that were not monitored with cameras.

DISCUSSION

We found that field-based methods of determining nest fate in our system were reasonably accurate at 84%. Similar measures of accuracy for estimates of nest fate have previously been reported (Pietz and Granfors 2000; Williams and Wood 2002; Ball and Bayne 2012). Accuracy of nest-fate assignment for passerines varied by nest fate and was lowest when nests were depredated (Ball and Bayne 2012). We found that the probability of correctly assigning nest fate was lowest when small mammals depredated nests, due to the presence of small eggshell fragments although confidence intervals around this estimate were large due to a small sample size ($n = 9$; Fig. 1-1a). However, successful nests were less likely to be correctly assigned than nests that were depredated by Coyotes, foxes, gulls, and Common Raven, though confidence intervals overlapped (Fig.1-1a). Determining nest fate for many species of shorebirds can be difficult because adults remove eggshell evidence soon after chicks hatch (Mabee et al. 2006) and we observed adults removing eggshells occasionally following depredation. Nest location could further alter the probability of correctly assigning nest fate. We documented a decrease in accuracy when nests were located on barren substrates, likely because eggshell evidence was more susceptible to disturbance from wind and precipitation, which makes it challenging to estimate relationships between habitat and nest survival.

Signs and evidence at nests may lead to incorrect assignments of nest fate. Depredated nests that were incorrectly assigned contained small fragments (80% of nests) and eggshell tops (30% of nests), which are both indicators of hatching (Mabee et al. 2006; Mabee 1997). Conversely, 64% of successful nests that were incorrectly assigned had no eggshell evidence and 27% had large eggshell pieces in the nest suggesting nest predation. Of our incorrect assignments for successful nests, 52% had incomplete clutches following partial depredation compared to 10% of correctly assigned nest fates. Traditional nest survival analyses consider a nest successful if at least one egg hatches. However, partial nest predation can create conflicting evidence leading to inconclusive assignments of nest fate (Lariviere 1999). As a result, the prevalence of partial nest predation is poorly understood in most systems (Lariviere 1999; Ackerman et al. 2003; Isaksson et al. 2007). In our study areas, partial predation was relatively common (19% of all successful nests).

There has been concern that nest predators could either be attracted to cameras or deterred by their presence creating potential bias when used. We did not detect a significant effect of cameras on nest survival rates (Fig. 1-2). Evidence suggests that rates of predation for shorebird nests are not greater when cameras are present (Liebezeit and Zack 2008; McKinnon and Bêty 2009; Demers and Robinson-Nilsen 2012) similar to evidence for passerines (Pietz and Granfors 2000; Richardson et al. 2009). Predators may identify visual and olfactory cues of observers when they repeatedly monitor nests that are not associated with cameras (Conover 2007), making cameras a method for minimizing disturbance.

When close attention is paid to nest age and evidence at nests, traditional protocols for determining nest fate are effective, particularly given that we did not detect a difference in the probability of correct assignment among individual observers (Mabee 1997; Williams and Wood 2002; Mabee et al. 2006; Ball and Bayne 2012). The most conservative method for assigning nests as successful is to locate chicks, however because shorebirds often leave their nest within hours of hatching, this method can be impractical. Additional time spent in the field describing nest conditions or collecting nest substrate to be sorted in a lab setting may aid in locating small eggshell fragments after hatching. An effort to check nests more often as anticipated hatch date approaches may also increase the accuracy of assigning nest fate (Williams and Wood 2002; Ball and Bayne 2012), but could induce deleterious effects on rates of predation from increased presence at the nest by observers. Remote cameras provided unambiguous data regarding nest predators and nest fate. If it is not feasible for all nests to be monitored with remote cameras, we suggest using cameras on a subset of nests to identify predators and characterize eggshell evidence in the field that may be specific to each system.

Table 1-1. Number of Snowy Plover nests monitored with cameras, number of correct assignments of nest fate, and total number of nests monitored at Great Salt Lake and in western Utah between 2011 and 2016.

Site	Year	Camera	Correct assignments	Total nests
Western Utah	2011	6	6 (100%)	9
Western Utah	2012	12	10 (83%)	18
Great Salt Lake	2013	2	2 (100%)	2
Western Utah	2013	7	6 (86%)	22
Great Salt Lake	2014	50	39 (78%)	124
Western Utah	2014	42	36 (86%)	52
Great Salt Lake	2015	43	40 (93%)	63
Western Utah	2015	25	23 (92%)	36
Great Salt Lake	2016	54	45 (83%)	74
Western Utah	2016	100	80 (80%)	108
Total		341	287 (84%)	508

Table 1-2. Ranking of 16 a-priori logistic regression models used to identify variables influencing accuracy of nest-fate assignment for Snowy Plover. The predator covariate represented nest predation by Coyote *Canis latrans*, foxes (Kit Fox *Vulpes macrotis* and Red Fox *Vulpes vulpes*), gulls *Larus* spp., Common Raven *Corvus corax*, small mammals (White-tailed Antelope Ground Squirrel *Ammospermophilus leucurus* and unidentified mice), and successful nests as a reference. Observer (n = 5) and nesting substrate (barren ground, vegetation, or debris) were also included as categorical independent variables. The number of days between hatch date and last date checked by observers (NDays) and nest age (z-score standardised) were included as continuous independent variables. K denotes the number of parameters in a model, wi the Akaike model weight, and LL the log-likelihood.

Model	ΔAIC_c	w_i	LL	K
Predator + Nest Age	0	0.51	-132.84	7
Predator + Substrate	1.91	0.19	-132.75	8
Predator	2.73	0.13	-135.25	6
Nest Age	4.38	0.06	-140.18	2
Predator + NDays	4.48	0.05	-135.08	7
Predator + Observer	5.38	0.03	-139.66	7
NDays + Nest Age	6.68	0.02	-139.29	3
Observer + Nest Age	9.75	0	-137.71	3
Substrate + Nest Age	10.71	0	-133.96	4
Intercept-only	19.99	0	-149	1
Observer	21.07	0	-148.52	2
NDays	23.23	0	-148.58	2
Observer + NDays	24.22	0	-145.99	3
Substrate + Observer	24.42	0	-148.16	4
Substrate	25.11	0	-145.39	3
Substrate + NDays	26.73	0	-145.15	4

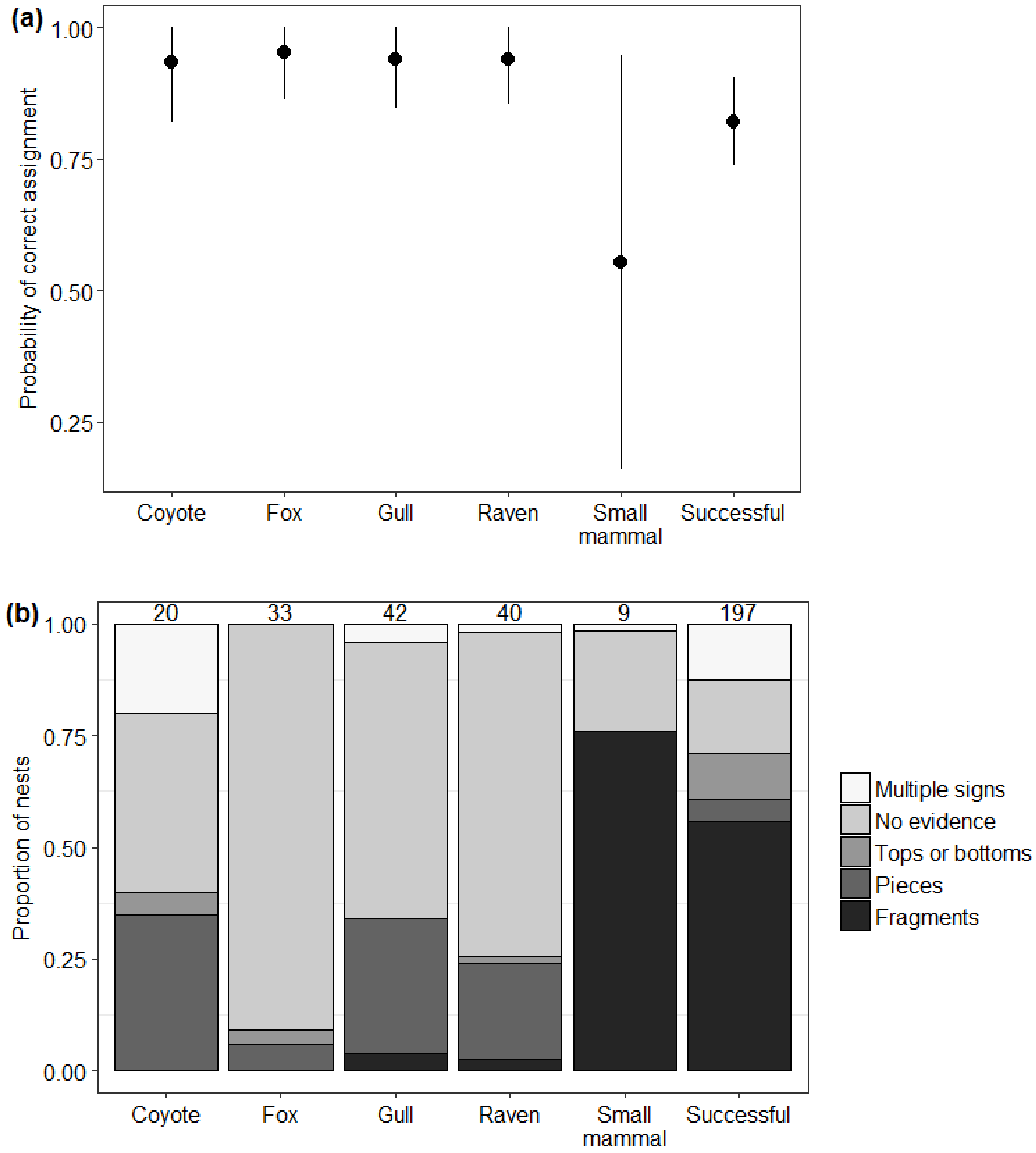

Figure 1-1. Probability (± 95% confidence interval) of correctly assigning Snowy Plover nest fate for depredated nests according to each predator group (columns 1-5) and successful nests (last column) using the mean for each covariate from our model-averaged set (a). Proportion of eggshell evidence present at depredated and successful nests (b). Eggshell fragments were 1–5 mm and eggshell pieces were ≥ 6 mm. Multiple signs represent the presence of more than one

type of eggshell evidence. Sample size for each group is represented above bars. Predator groups include Coyotes *Canis latrans*, foxes (Red Fox *Vulpes macrotis* at Great Salt Lake and Kit Fox *Vulpes vulpes* at western Utah sites), gulls *Larus* spp., Common Ravens *Corvus corax*, and small mammals (White-tailed Antelope Ground Squirrels *Ammospermophilus leucurus* and unidentified mice).

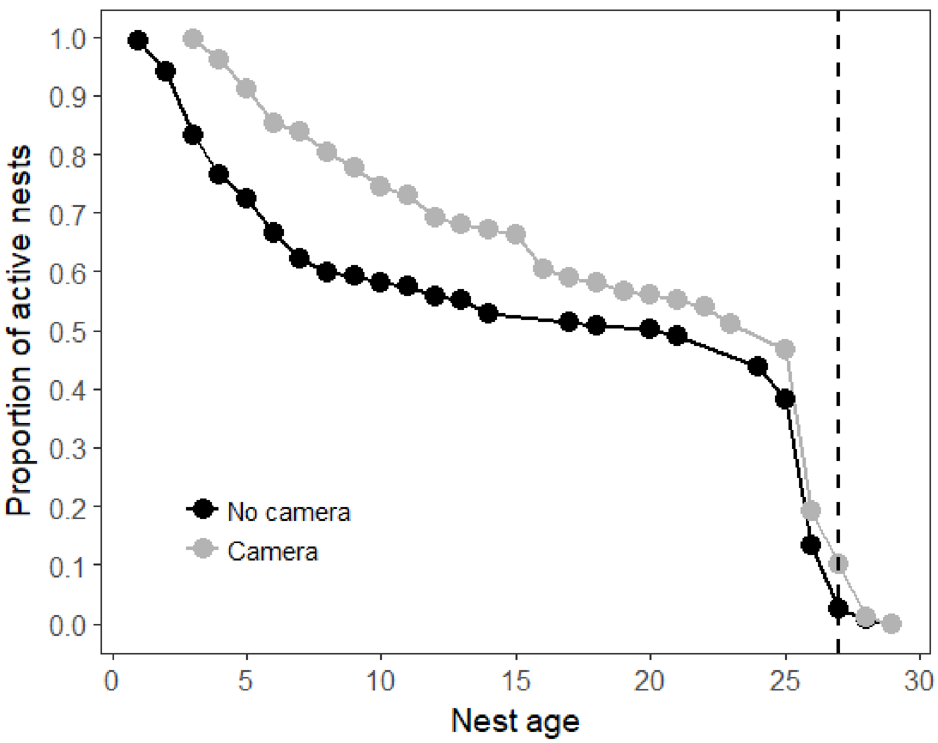

Figure 1-2. Proportion of active nests across the incubation period for nests monitored with and without cameras. We did not begin monitoring nests with cameras until 4 days after the onset of incubation to minimize the risk of abandonment. The dashed line corresponds with the mean incubation period in Snowy Plovers (27 days).

CHAPTER 2: THE IMPORTANCE OF FUNCTIONAL RESPONSES AMONG COMPETING PREDATORS FOR AVIAN NESTING SUCCESS[2]

SUMMARY

The relationship between the rate of predation and prey abundance is an important component of predator-prey dynamics. However, functional responses are less straightforward when multiple predators compete for shared prey. Interactions among competing predators can reduce or enhance effects of predation on prey populations. Because many avian populations experience high rates of nest predation, understanding the role of specific predators on nest mortality will lead to more informed conservation and management strategies which attempt to increase productivity by removing certain predators or managing habitat to limit their impact. Our goal was to evaluate effects of specific predators and the influence of nest abundance on nest mortality. We monitored snowy plover *Charadrius nivosus* nests across 7 years at two study areas in Utah, USA with remote cameras. We modeled predator-specific hazard rates for nest mortality in a Bayesian framework to assess relationships between competing predators and the role of nest abundance on predator-specific hazard rates. We found that hazard rates for nest mortality by gulls *Larus* spp. decreased with increasing nest abundance, whereas nest mortality by foxes *Vulpes* spp. and ravens *Corvus corax* initially increased, indicating that dietary switching may occur when nests become more abundant. Nest mortalities of specific predators were often not independent and ranged between compensatory (e.g., mammalian mesopredators),

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and over-additive (e.g., avian predators) across the breeding season. The non-independence between nest mortalities suggests that reductions in some predators may not translate to additive increases in overall nest success. Analyses of cause-specific mortality are rarely applied to avian nests, but examination of interacting impacts among competing predators on nest survival may provide insight into specific drivers of avian population dynamics.

INTRODUCTION

Across most ecosystems, species distributions and abundances are changing as a result of human-modified landscapes and climate change (Sala et al. 2000; Chen et al. 2011). Predicting the impacts of these changes on individual populations can be confounded by indirect effects of biotic interactions including competition and predation (Sih et al. 1985; Holt and Lawton 1994). Predation plays a pivotal role in shaping most ecosystems yet varying morphological traits, habitat use, and foraging behaviors among multiple predator species can collectively produce weakened or enhanced effects on prey relative to predictions from summing the individual effects of predators (Sih et al. 1998; Chalcraft and Resetarits 2003; Schmitz 2007; McCoy et al. 2012; Vance-Chalcraft and Soluk 2005). Predators not only interact with prey but are often forced to interact with one another through competition (e.g. interference or exploitative) or intraguild predation (Griffen and Byers 2006; Polis et al. 1989). Further, species within a trophic position in predator communities may not be functionally substitutable in the food web (Chalcraft and Resetarits 2003). Consequently, characterizing the functional role of specific predators and combinations of competing predators is key to developing predictive theories of how predators drive changes in prey populations.

An essential starting point for assessments of predator-prey dynamics is the relationship between prey abundance and rate of consumption (i.e., the functional response) (Solomon 1949;

Holling 1959). The rate at which predators consume prey is determined by time spent searching for and handling prey and variation in these rates results in different patterns of the functional response (Holling 1959). A linear (Type I) functional response represents a consumption rate that increases proportionally with prey availability (Jeschke et al. 2004). The most widely and frequently observed functional response is a hyperbolic (Type II) curve, reflecting declining predator efficiency with increasing prey density (Jeschke et al. 2004; Berryman 1992). Alternatively, sigmoidal (Type III) functional responses involve a consumption rate that increases across a range of low to intermediate prey densities and declines at higher prey densities (Hassell 1978). These sigmoidal responses are often attributed to predators that switch prey depending on prey density (Murdoch 1969), predator learning (Holling 1959; Hassell 1978), and prey refuges from predation (Hossie and Murray 2010). Research on functional responses in ecology has largely focused on single-predator systems, often in controlled experimental settings, and relatively few have examined the effects of interactions among predators on density-dependent prey consumption. Competition for shared prey resources between interspecific predators can weaken the link between prey availability and predation rate (Arditi and Ginzburg 2012; Abrams and Ginzburg 2000). Thus, there is an increasing interest in how competing predators respond to prey availability and if the predictions from theoretical models of predator-prey dynamics are realized in wildlife populations under natural conditions (Wasserman et al. 2016; Schmitz et al. 2017; Chan et al. 2017).

Scenarios with multiple predators competing for prey can be considered competing risks because prey mortality can only happen once per individual. Appropriate analyses of cause-specific mortality allow for estimates of marginal risks of one cause while accounting for competing sources (Heisey and Patterson 2006). These assessments can be used to examine functional responses among competing predators resulting in mortality hazard rates for specific predators that can be compared to explain their additive or compensatory effects on overall prey mortality. Multiple sources of mortality can be compensatory or additive, however these sources may fall along a continuum of alternative hypotheses, including over-compensation, partial compensation, and superadditive (Servanty et al. 2010; Sandercock et al. 2011). Although the additive and compensatory mortality hypotheses typically compare effects of harvest and natural mortality (Burnham & Anderson 1984; Boyce, Sinclair & White 1999; Servanty *et al.* 2010; Sandercock *et al.* 2011; Koons, Rockwell & Aubry 2014), these concepts can provide insight for interactions between competing predators. Mechanisms underlying compensatory predation are thought to arise from interspecific competition and varying foraging efficiencies (Henke and Bryant 1999; Murphy and Bradfield 1992; Hubbs and Boonstra 1997). For example, reductions in the abundance of a larger predator may lead to the release of smaller meso-predators, which are typically limited through direct predation by the larger predator, competition for resources, or temporal and spatial avoidance of the larger predator (Crooks and Soule 1999; Cote and Sutherland 1997). Thus, understanding competing risks of predation can provide mechanistic insight into the potential effectiveness of predator management for conserving prey.

Predation on avian nests has been identified as the primary source of reproductive loss for a wide range of species and across a diversity of habitats (Martin 1993; Ricklefs 1969). Yet, little work has been done assessing the role of competition amongst predators on nest mortality and how specific predators functionally respond to nest availability. Compensatory nest predation has ramifications for management strategies that attempt to increase productivity by removing nest predators. For example, when the abundance of a given predator is reduced, overall nest mortality could remain constant if nest predation shifts to other predators (Ellis-Felege et al. 2012; Errington 1967).

In this study, we compared the forms of functional responses of specific predators to the availability of snowy plover (*Charadrius nivosus*) nests at two study areas with differing predator communities. We then estimated the degree of correlation between predator-specific hazard rates of nest mortality to assess their compensatory vs. additive effects on total hazard rates of nest mortality. Our study provides a unique example of how combining competing risks of mortality with functional responses within a Bayesian framework can be a flexible approach for researchers broadly interested in predator-prey dynamics when there are multiple competing predators.

Snowy plovers are an ideal model species to investigate questions of predator-specific nest mortality because most populations are vulnerable to a suite of avian and mammalian predators, and nest predation is common (Ellis et al. 2015; Page et al. 2009). Foraging strategies differ between avian (diurnal activity using visual cues of nests or activity of adults) and mammalian predators (largely nocturnal relying on olfactory cues and systematic searching), which may differentially influence their effects on nest mortality (Schmidt 1999). We predicted that avian and mammalian predators would differ in the shape of their functional responses and that avian predators would be more efficient than mammalian predators when nests were rare (early and late in the breeding season) because of greater encounter rates (Schmidt 1999). We also predicted that competing predators would lead to some instances of compensatory predation on snowy plover nests due to varying foraging efficiencies (e.g., between avian and mammalian predators) or interspecific competition (e.g., between mammalian predators). Understanding the dynamics of nest predation will become increasingly complex with changes in species' distributions in conjunction with other environmental stressors (Ibáñez-Álamo et al. 2015). Consequently, relating interactions among competing predator species to nest survival is needed to better understand changes in avian populations and resulting effects on biodiversity.

METHODS

Study Areas and Data Collection

This study was conducted at two areas in Utah, USA: western Utah, and Great Salt Lake. The western Utah study area included the following sites: Fish Springs National Wildlife Refuge (39°51’01” N, 113°23’45” W; 2011 – 2017), the United States Army Dugway Proving Ground (39°56’14” N, 113°25’20” W; 2011 – 2017), and Blue Lake (40°30’11” N, 114°00’55” W; 2016 – 2017). Fish Springs National Wildlife Refuge covers 36 km^2 of marsh habitat fed by several thermal springs (Stolley et al. 1999). Spring water flows from Fish Springs National Wildlife Refuge onto the alkaline flats of the United States Army’s Dugway Proving Ground, providing approximately 200 km^2 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. In western Utah, the occupancy of snowy plovers is low and associated with scarce 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.

We also collected data along the eastern edge of Great Salt Lake at two sites: Saltair (40°46’00” N, 112°09’50” W) and Antelope Island State Park (41°05’08” N, 112°08’08” W) 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 the largest breeding population 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 (Cavitt et al. 2014; Conover 1983) provide multiple challenges to the conservation of snowy plovers and other shorebirds. 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.

We conducted nest surveys at least once per week at each site during the breeding season (early April – mid August) (Ellis et al. 2015; Paton 1995) to locate new nests and determine the status of extant nests. Once nests were located, we floated eggs to estimate incubation stage and initiation date assuming an egg-laying period of 3 days and a 27-day incubation period (Paton 1995; Page et al. 2009). To determine nest fate and identify predators, we used Reconyx PC900 infrared-triggered cameras (Reconyx, Inc., Holmen, Wisconsin). Cameras were attached to stakes, placed approximately 2 m away from nests, and were elevated 15 – 30 cm above the 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 *Larus* spp., 2) Common Raven *Corvus corax*, 3) coyotes *Canis latrans*, 4) foxes (red foxes *Vulpes vulpes* at Great Salt Lake sites and kit foxes *Vulpes macrotis* at western Utah sites) and 5) other (white-tailed antelope ground squirrels *Ammospermophilus leucurus*, unidentified mice, Northern Harriers *Circus* *cyaneus*, and raccoons *Procyon lotor*). We removed 11 nests from our sample due to unclear photos or camera failure, however we are confident that our assignments of nest predators were accurate due to the openness of the habitat and amount of time predators spent at nests consuming eggs. 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.

Analysis

Competing Risks of Nest Mortality Model

Analyses of cause-specific nest mortality are uncommon for several reasons. Until the advent of infrared-triggered cameras, it was difficult to accurately assess the source of nest predation (Lariviere 1999). In addition, relatively few analytical methods are available that account for discovery bias (Mayfield 1961) and simultaneously allow for the incorporation of covariates (Etterson et al. 2007; Devineau et al. 2014) and random effects (Darrah et al. 2017). Within a Bayesian framework, we used a cause-specific hazard model to estimate competing sources of nest mortality (Heisey and Patterson 2006), which is more appropriate for many types of inference than cause-specific mortality probabilities due to the intrinsic negative correlation of mortality probabilities (Schaub and Lebreton 2004; Ergon et al. 2018). Nest exposure days began the day the camera was placed at the nest, which provides a conservative estimate of daily survival probability for nests monitored with cameras (McKinnon and Bêty 2009). We right-censored abandoned and flooded nests because we were primarily interested in dynamics of nest predation (nests were included and considered successful until the date before it failed). Our model took the following form:

$$y_i \sim Multinomial\big(S, P_j, 1\big) \tag{1}$$

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

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 *J* causes of predation by predator *j* (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).

We first fit a reference model where predator-specific hazard rates were estimated with a random intercepts parameterization through a log-link:

$$\log\big(h_j^{s,r,t}\big) = a_j^s + \varepsilon_j^{r,s} + \gamma_j^{t,s}, \;\; \varepsilon_j^{r,s} \sim Norm\big(0, \sigma_j^{2,r,s}\big), \; \gamma_j^{t,s} \sim Norm(0, \sigma_j^{2,t,s}) \tag{2}$$

where each a_j^s represents the fixed-effect mean for predator-specific hazard rates at each study area *s* (Great Salt Lake and western Utah). Year *r*, and day of season *t* were included as study area-specific random effects ($\varepsilon_j^{r,s}$ and $\gamma_j^{t,s}$, respectively) to account for temporal variation in predator-specific nest mortality, which were each modeled using a normal distribution with a mean of zero and variance $\sigma_j^{2,r,s}$or $\sigma_j^{2,t,s}$, respectively.

Seasonal Model for Non-stationary Variation in Nest Mortality

To assess within-season patterns of predator-specific nest mortality, we used an autoregressive process (AR model) similar to that used by Cross et al. (2015) and Koons et al.

(2019), which describes empirical patterns not based on theoretical predictions. Estimates of daily predator-specific nest mortality depended linearly on the previous day and stochastically:

$$h_j^t \sim Norm(h_j^{t-1}, \omega_j^t) \tag{3}$$

with ω_j^t as a variance term for the effect that allowed for daily random deviations from lag-1 autocorrelation. The AR model also incorporated a random effect associated with each year for each predator-specific mortality, $\varepsilon_j^{r,s}$, with the same description as Eqn. 2. We allowed nest mortality hazard rates to vary between study areas to assess whether seasonal patterns were site-specific. Nests that were depredated by predators in the 'other' category were modeled as an intercept-only with no seasonal or annual variation because there were relatively few observations in this category (3% of total nests). Nest predation by gulls occurred only at Great Salt Lake, so seasonal and annual variation was estimated at a single site for this cause of failure.

Predator Functional Response to Nest Density

To categorically define the functional response types of specific predators to the availability of snowy plover nests, we evaluated the shape of the relationship between nest mortality hazards and nest abundance. We first estimated an index of snowy plover nest abundance on each day of the breeding season using a Horvitz-Thompson estimator (Dinsmore et al. 2002; Grand et al. 2006; Miller et al. 2006). The estimator assumes that if nests were not destroyed, they were eventually found prior to hatching and that nests initiated on the same day had similar probability of being discovered. To adjust the number of nests initiated on each day, we used estimates of daily survival probability from the AR model which was calculated as $S^t = e^{-\sum_{j=1}^{J} h_j^t}$ (Ergon et al. 2018). For each nest, we computed the inverse of the product of daily survival probabilities from when the nest was initiated until it was discovered from each MCMC sample. This process resulted in an adjusted number of nests that would have been discovered had they survived, and that were initiated on the same day the found nest was initiated. We summed the frequencies of the adjusted number to estimate a distribution of expected number of active nests for each day of the breeding season. We then calculated an adjusted mean and associated standard deviation which were included as an ‘uncertain’ covariate in the analyses of nest mortality, assuming a normal distribution of the posterior samples.

We used the reference nest mortality model (Eqn. 2) with the addition of polynomial terms for estimates of daily nest abundance (with associated uncertainty) to evaluate the form of predator functional responses. Our functional response model included linear, quadratic, and cubic terms to provide an adequate fit for both Type II and Type III curves (Trexler et al. 1988). Nest abundance was scaled to have a mean of zero and standard deviation of one after squaring and cubing to limit multicollinearity. Polynomial logistic regression (i.e., the proportion of prey eaten) as a function of prey availability produces distinct Type II and Type III curves (initially decreasing or increasing, respectively) (Juliano 2001). If the linear coefficient (β_1) is > 0 and the quadratic coefficient (β_2) is < 0, the proportion of nests consumed is positively density dependent, describing a Type III functional response. If $\beta_1 < 0$, the proportion of nests consumed declines monotonically, thus describing a Type II response (Juliano 2001). In Type I functional responses, the proportion of nests consumed remains constant with increasing nest abundance (Juliano 2001). For reasons described above, we did not fit our cause-specific mortality models using a multinomial logit link and did not use probabilities for basing inference (see also Ergon et al. 2018), but the predicted relationships between prey hazards (risks of mortality) and prey availability for Type II and III functional responses are qualitatively similar.

Assessing the Overall Effects of Predator-Specific Nest Mortality

To test for independent vs. dependent relationships among predator-specific nest mortality hazard rates, we used daily estimates for an average year from the AR model described above. The degree of correlation between two time-dependent risks of mortality can be used to assess whether different sources of mortality are compensatory, partially compensatory, additive, or over-additive (Servanty et al. 2010). If predator-specific hazard rates vary independently across the breeding season, the correlation would be close to zero and the two mortality types would be additive. Alternatively, if predator-specific hazard rates are negatively correlated, their effects will be compensatory on overall nest mortality. When over-additivity occurs, the correlation is positive indicating that both sources of mortality are increasing concurrently (Servanty et al. 2010; Ergon et al. 2018).

We evaluated the degree of correlation between all pairs of predator-specific nest mortality hazards across each day of the breeding season. Using the *cor* function in R (R Development Core Team 2018), we calculated Pearson's correlations between Markov chain Monte Carlo (MCMC) samples for every pairwise combination of h_j^t to derive posterior distributions of correlated relationships. From these distributions we calculated an overall correlation value across the breeding season, and separate correlations for early and late periods in the breeding season based on when 50% of the nests had been laid. In addition, we calculated the correlation between predator-specific hazards and the overall nest mortality hazard ($\sum_{j=1}^{J} h_j^t$) across the breeding season to examine the net impact (or lack thereof in the case of compensation) of specific predators on the overall nest mortality hazard (Sandercock et al. 2011; Ergon et al. 2018). We applied the correlation analyses to each site separately because of differing predator communities.

Proportion of Seasonal Variance Explained

To quantify the proportion of process variation pertaining to seasonal variability in our mixed-effects models that could be predicted by explanatory variables, we calculated R^2_Var (Franklin et al. 2000; Grosbois et al. 2008). This statistic can be considered analogous to the coefficient of determination (the proportion of a variance component explained) and is calculated as:

$$R^2\_Var = \frac{\hat{\sigma}_j^{2,t,s}(ref) - \hat{\sigma}_j^{2,t,s}(focal)}{\hat{\sigma}_j^{2,t,s}(ref)} \tag{4}$$

using estimated random variance from the day of season random effect in the reference model (Eqn. 2, ref) with the same variance component from focal models (AR and functional response models) to generate R^2_Var for each focal model.

Estimation

Parameters in the nest mortality models were estimated using a Bayesian application of MCMC sampling, implemented in JAGS (Plummer 2017) and cast in R via the package *jagsUI* (Kellner 2015). We chose vague priors for all parameters including a uniform [0, 10] distribution for variance hyperpriors, and a normal distribution with mean 0 and standard deviation of 10 for initial conditions in the AR model, all intercepts, and fixed-effect covariates from the polynomial model. We generated three MCMC chains and assessed convergence using the Gelman-Rubin diagnostic $\hat{R}$ (Gelman et al. 2004) and visual inspection of trace plots. For all models, convergence was achieved for estimated parameters (all $\hat{R} < 1.1$, with trace plots showing mixing among stationary MCMC chains). We scored the predictive ability of models relative to one another using WAIC (Watanabe 2010) by monitoring log-likelihoods for the y_i and then applying the *waic* function in the *loo* package for R (Vehtari et al. 2018). The number of iterations, thinning rate, burn-in, and adapt periods for each model, as well as R code for each model is provided in the Appendix.

RESULTS

Across our two study areas, we monitored 473 nests with remote cameras with 194 nests from Great Salt Lake and 279 nests from western Utah used for analyses of predator-specific nest mortality (see Table S1 for more detail). Daily nest mortality hazard rates from the reference model indicated that the most dominant nest predator at Great Salt Lake was ravens, with an estimated hazard rate that was 2.3, 4.3, and 5.9 times greater than rates for gulls, red foxes, and coyotes, respectively (Table S2). Alternatively, in western Utah, kit foxes had the greatest nest mortality hazard rate, which was 3.3 and 3.7 times greater than rates for coyotes and ravens, respectively (Table S2). Nest survival was variable across the study period, but baseline nest success (across a 27-day incubation period) from the reference model was lower at Great Salt Lake (µ: 0.33, 95% BCI: 0.15 – 0.54) than in western Utah (0.73, 0.58 – 0.84). Residual annual variation in nest mortality was greatest for ravens in western UT (standard deviation = 2.12, but 0.66 at Great Salt Lake) compared to 0.81 for gulls at Great Salt Lake, 0.76 and 0.62 for coyotes, and 0.55 and 0.24 for foxes at Great Salt Lake and western Utah, respectively. The AR model (WAIC = 2290.8) provided the best fit to the data relative to the reference model (WAIC = 2378.3) and the functional response model (WAIC = 2360.9).

For gulls, nest mortality hazard rates declined ($\beta_1^g < 0$ with 95% BCI that did not overlap 0) with increasing nest abundance suggesting a Type II functional response (Fig. 2-1, Table S3). Alternatively, hazard rates for foxes and ravens initially increased with nest abundance ($\beta_1^{f,r} > 0$, $\beta_2^{f,r} < 0$) and both 95% BCI did not overlap 0, suggesting statistical support for Type III functional responses of these predators to the availability of snowy plover nests. Across the range of observed nest abundances, eventual satiation in foxes was weakly supported, but supported in gulls, and ravens (Fig. 2-1). Hazard rates of nest mortality for coyotes appeared to decrease with nest abundance (Fig. 2-1), however 95% BCI overlapped 0 for $\beta^{c}_{1,2,3}$, with mean estimates centered at 0 (Table S3), suggesting that nest mortality by coyotes was either dominated by a Type I (linear) functional response or that coyote predation events were too rare for rigorously estimating their functional response to the availability of snowy plover nests. R^2*_Var* suggested that polynomial terms for nest abundance (i.e., predator functional responses) explained between 19 and 87% of the seasonal variability in predator-specific nest mortality, although most estimates of R^2*_Var* were on the higher end of that range (Table 2-1).

Estimates of predator-specific hazard rates of nest mortality from the AR model indicated that phenological peaks in the hazard rate varied with species of predator (Fig. S1). While R^2*_Var* suggested that autoregressive smoothing explained between 80 and 91% of the seasonal variability in predator-specific nest mortality, we note that these are phenomenological descriptions (Table 2-1). The correlations between predator-specific hazard rates varied and supported partially compensatory, additive, and over-additive hypotheses depending on predator comparisons and time of breeding season (Fig. 2-2). The mass of the posterior distribution of correlations between fox and coyote hazard rates were centered on negative values at all time periods and study areas, indicating partially compensatory impacts because they were not directly -1 (Fig. 2-2). Correlations between avian and mammalian predators, were negatively correlated early in the season but relationships became additive late in the season, with the exception of ravens and coyotes in western Utah. For this predator combination the correlation was negative late in the breeding season but additive otherwise. Over-additive nest mortality occurred between ravens and gulls, particularly early in the nesting season.

At Great Salt Lake, hazard rates for gulls and ravens were positively correlated with the total hazard rate indicating that increasing nest mortality from these avian predators had net additive effects (Fig. 2-3). Nest mortalities by foxes and coyotes were not strongly correlated with the total hazard rate (95% BCI overlapped zero), indicating that their net effects were compensatory. Alternatively, in western Utah, hazard rates for foxes were positively correlated with the total hazard rate suggesting additive effects, while hazard rates for ravens and coyotes were positively correlated but 95% BCI overlapped zero (Fig. 2-3).

DISCUSSION

Understanding the influence of prey availability on predator-specific mortality is important for evaluating the dynamics of prey survival and predicting the effects of changing predator regimes. Using snowy plover nests and their predators as an example system, our study provided evidence that predator-specific nest mortalities varied with nest abundance and were rarely independent from one another throughout the breeding season. Predator species responded differently to nest abundance resulting in different functional response shapes. Because the functional roles of nest predators differed, there is a need to evaluate predator-prey dynamics in a multispecies context. While previous work has shown that compensation between nest predators can occur on an annual time-scale (Ellis-Felege et al. 2012), we have shown that these interactions can occur at finer scales within the breeding season of a single year.

The dominant nest predators in our study have generalist diets (Byerly et al. 2017; Roberts 2013; Stiehl and Trautwein 1991), and a pulsed resource, like shorebird nests, likely does not comprise a large proportion of their overall diets. One assessment of gull stomachs at the Great Salt Lake indicated that avian eggs and chicks comprised only a small proportion of gull diets during the breeding season (< 5%) (Greenhalgh 1952). Although we documented nest predation by kit fox and coyotes, avian eggs were not found in the scats of these predators in western Utah during the same time period as our study, suggesting avian eggs comprise a small part of their diet as well (Byerly et al. 2017). Thus, indirect effects of alternate prey on nest predation presumably exist that we did not evaluate, and one might expect that we would detect dietary switching (McKinnon et al. 2014; Ackerman 2002). Our results indeed supported a Type III functional response for foxes and ravens, suggesting dietary switching or predator learning, when nest abundance was low. The traditional view in natural systems is that predators consistently become satiated at high prey densities (Jeschke et al. 2004), which was apparent in gulls and ravens. Across the range of observed nest abundances, satiation was weakly supported for foxes and may have been limited due to competitive interactions with coyotes (i.e., negative correlation between nest mortalities by foxes and coyotes). Alternatively, foxes may have cached eggs which relaxed their satiation (Ralls and White 1995). Coyotes most supported a Type I, linear, functional response, which are rarely observed in experimental settings and largely attributed to filter feeders, because handling and digestion time are not limiting (Jeschke et al. 2002). Type I responses have been observed in a lynx-squirrel system (Chan et al. 2017), and in these cases the predator may not capture the prey at sufficiently high rates to experience satiation (i.e., they consume the prey incidentally).

The Great Salt Lake was dominated by avian predators and the Great Salt Lake hosts some of the largest colonies of California gulls *Larus californicus* in the interior west of North America (Cavitt et al. 2014; Conover 1983). While we predicted that avian predators would exhibit similar functional responses to nest availability, our results suggested gulls had a Type II response, whereas ravens had a Type III response. While both ravens and gulls are generalist omnivores, ravens may have depended on alternative food sources at low nest densities more so than gulls. Ravens and gulls had additive effects on the total hazard of nest mortality at the Great Salt Lake and corvids in general have been identified as primary nest predators for many ground-nesting species (Burrell and Colwell 2012; O'Neil et al. 2018; Gibson et al. 2018; Madden et al. 2015), whereas gulls may be an atypical shorebird nest predator (Page et al. 1983). Raven and gull hazard rates were positively correlated early in the breeding season, suggesting that their combined effects were over-additive (Liermann and Hilborn 2001; Servanty et al. 2010; Creel and Rotella 2010). The positive correlation between hazard rates of two nest predators might be generated by different mechanisms: both gulls and ravens are visual predators and may develop similar search images based on nests, incubating adults, or cues from the other predator species (Ishii and Shimada 2009), or the presence of either avian predator may elicit behavioral response (e.g., broken-wing displays) by incubating snowy plovers leading more visual predators to nesting areas (Smith and Edwards 2018; Gómez-Serrano and López-López 2016).

We found the strongest compensatory relationships throughout the nesting season between kit foxes and coyotes in western Utah, supporting our prediction of interspecific competition. Competition for habitat and food resources has been documented between kit fox and coyotes (Arjo et al. 2007; Nelson et al. 2007; Byerly et al. 2017; Cypher and Spencer 1998), with a clear dominance hierarchy of coyotes negatively affecting the subordinate species (foxes). Coyotes also represent a primary source of mortality in some kit fox populations (Ralls and White 1995; Kozlowski et al. 2008; Kluever and Gese 2017). Peaks in nest mortality by kit foxes occurred earlier in the year relative to coyotes, indicating kit foxes may alternatively contribute to compensatory nest predation with coyotes via exploitation competition. The impact of early- to mid-season nest mortality by kit foxes was strong enough to elicit an additive effect on the total hazard rate in western Utah. The net impact of nest mortality by coyotes later in the season, however, was compensatory, indicating that reducing coyote populations would have little effect on snowy plover nest survival and may have detrimental effects (Mezquida et al. 2006). Kit fox populations have declined since the mid-20th century with increased coyote abundance being linked as a driver (Arjo et al. 2007; Kozlowski et al. 2008). Thus, the additive effects of kit fox predation on snowy plover nest mortality and the designation of kit fox as a species of conservation concern may create conflict for managers of these two species.

Mammalian and avian nest predators had instances of compensatory relationships at some point during the nesting season, which partially supports our prediction of differing foraging efficiencies based on predator type. Avian predators primarily use visual stimuli (of the nest or incubating adults) which may lead to higher encounter probabilities than mammalian predators that use olfaction (Schmidt and Whelan 1998; Schmidt 1999; Bowman and Harris 1980), Consequently, foraging efficiencies within complex predator communities may fall along a spectrum, creating multiple avenues for compensation, however relatively little work has been done directly comparing foraging efficiencies between visual and olfactory nest predators, particularly for ground-nesting species.

Our models using cause-specific hazard rates to assess competing risks of nest mortality and predator-specific functional responses is a promising approach for ecological systems with multiple competing predators that may respond to prey abundance differently. Further, the flexible Bayesian framework allowed us to incorporate uncertainty around estimates of predictors (nest abundance). Our results suggest varied shapes of functional responses to nest abundance among the predator community, thus predators may differentially influence density-dependent processes contributing to population growth. In addition, we have shown that predator communities and associated effects on prey can be site-specific and therefore should be assessed locally. Plans involving the direct management of predators should be based on whether impacts of predation by certain species add to those of others, or if various interspecific interactions result in compensatory effects. When compensatory mechanisms exist in a food web, funding spent on direct management of predators will be ineffective while also diverting such funds away from methods that could be more effective (e.g., habitat management).

Table 2-1. Percentage of seasonal variance ($\hat{\sigma}_j^{2,t,s}$) in predator-specific nest mortality explained (R^2_*Var*) by functional responses (FR model) or autoregressive smoothing (AR model) relative to the reference model (Ref) for snowy plovers (*Charadrius nivosus*) at two study areas in Utah (2011-2017). Gulls were not responsible for nest predation events in western Utah.

		Great Salt Lake		Western Utah	
Model	Predator	$\hat{\sigma}_j^{2,t,s}$	R^2_*Var*	$\hat{\sigma}_j^{2,t,s}$	R^2_*Var*
Ref	Gull	1.31			
Ref	Raven	1.29		1.62	
Ref	Coyote	1.91		1.56	
Ref	Fox	0.75		1.47	
AR	Gull	0.21	0.84	-	-
AR	Raven	0.26	0.80	0.18	0.89
AR	Coyote	0.32	0.83	0.18	0.88
AR	Fox	0.08	0.89	0.13	0.91
FR	Gull	0.26	0.80	-	-
FR	Raven	0.28	0.78	1.31	0.19
FR	Coyote	0.79	0.59	0.90	0.42
FR	Fox	0.10	0.87	0.60	0.59

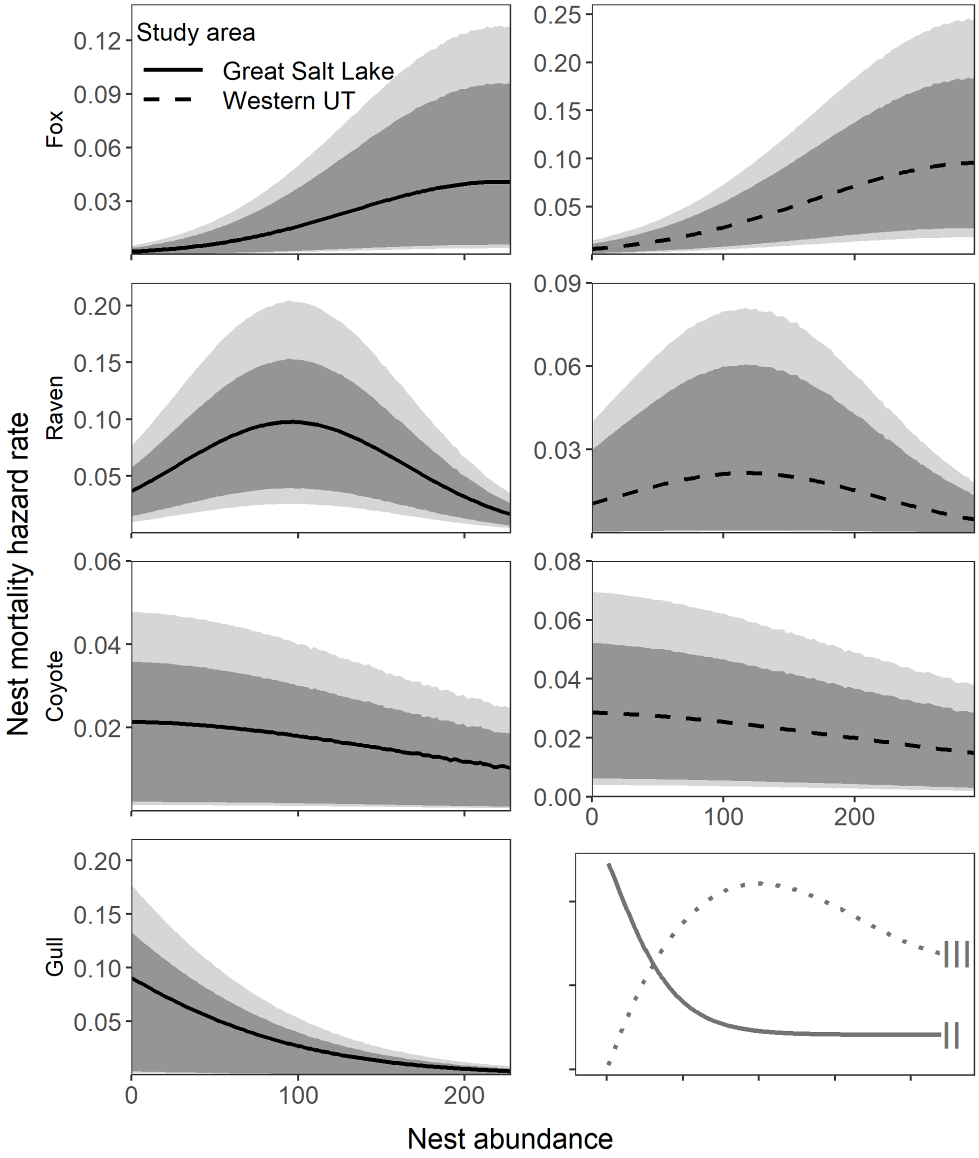

Figure 2-1. Functional responses of specific predators to snowy plover nest abundance at western Utah (right column, dashed lines) and Great Salt Lake (left column, solid lines). The bottom-right panel represents theoretical predicted curves for Type II (solid line) and III (dotted line) functional responses (adapted from Juliano 2001). Declining nest mortality with increasing nest abundance indicates a Type II response, whereas initially increasing nest mortality indicates a Type III response. Shaded areas represent statistical uncertainty (95% Bayesian credible interval) in predator-specific nest mortality hazards (darker shading) and estimated nest abundance.

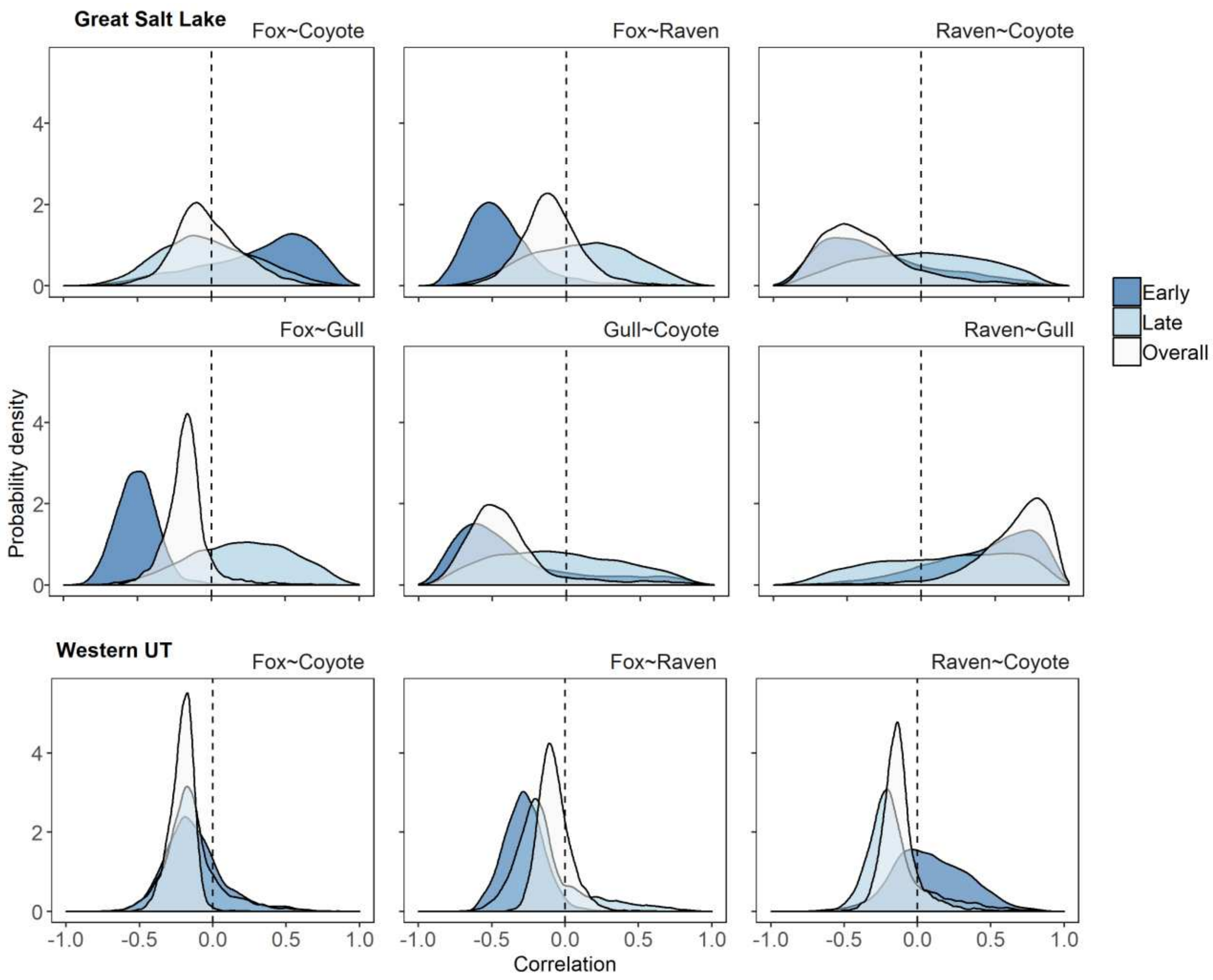

Figure 2-2. Posterior distributions of the correlation between each predator-specific combination of mortality hazard rates for snowy plover nests at two study areas. Negative correlations indicate compensatory effects on overall nest mortality, whereas correlations close to zero indicate that predator-specific hazard rates are additive to overall nest mortality. Positive correlations indicate over-additivity. The dashed vertical line references zero correlation. Early and late periods in the nesting season were separated by the date when 50% of nests had been laid according to estimated nest abundance, which corresponded with 13 June at Great Salt Lake and 5 June in western Utah.

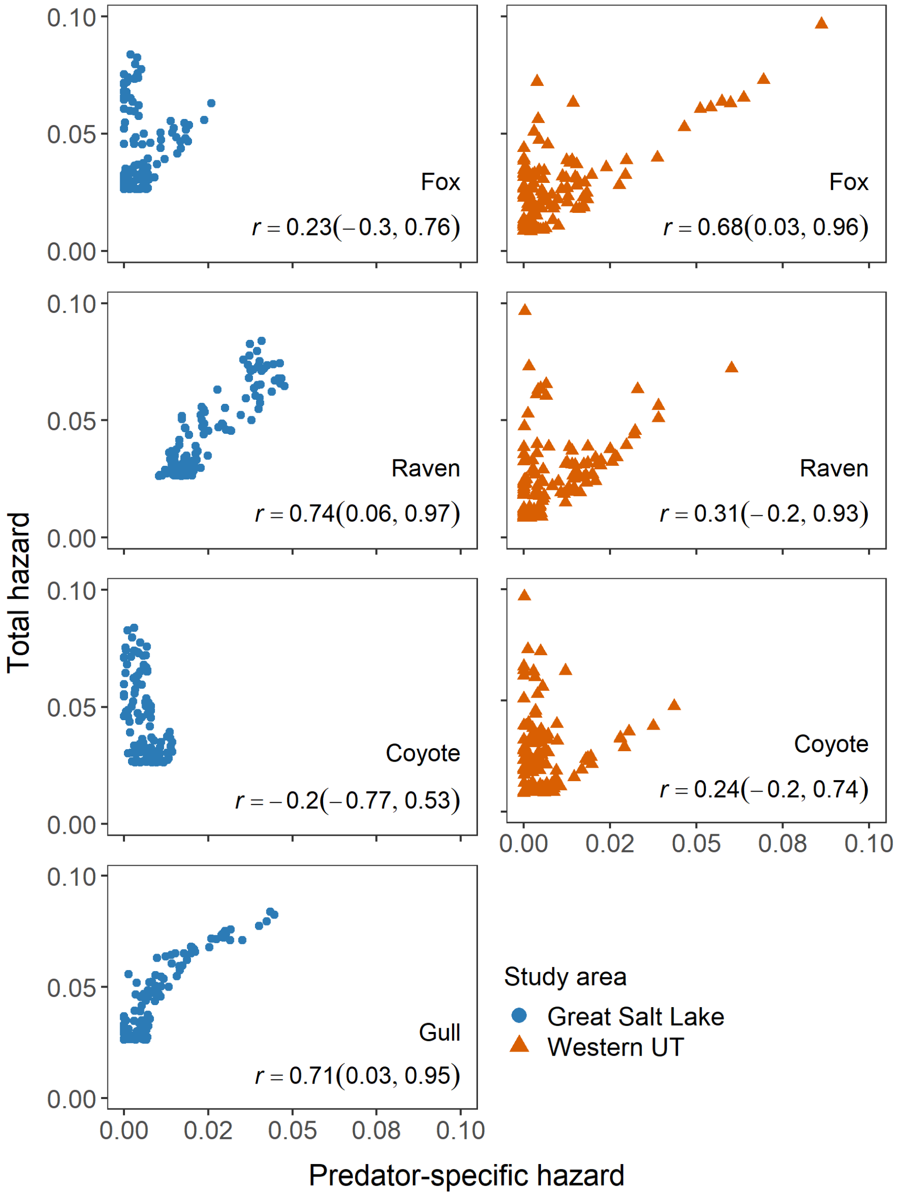

Figure 2-3. Relationships between hazard rates of predator-specific mortality and the total hazard rate for snowy plover nests (Pearson's correlation, *r*, with 95% Bayesian credible intervals shown in parentheses). A positive correlation between predator-specific hazard rates and total hazard rate indicates that mortality is additive, whereas zero correlation indicates that mortality is compensatory.

CHAPTER 3: SCALE-DEPENDENCE IN HABITAT ASSOCIATIONS WITH CAUSE-SPECIFIC PREDATION OF SNOWY PLOVER NESTS

SUMMARY

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, and 2.5 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 dispersal) 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.

INTRODUCTION

Wildlife species interact with and perceive the environment at different spatial scales, thus understanding ecological processes is inherently dependent on the spatial scale at which habitat structure is measured (Levin 1992; Wiens 1989). 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 (Stuber et al. 2017; Jackson and Fahrig 2015). 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 compete for a common set of nests. 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 (Stephens et al. 2004; Chalfoun et al. 2002). 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 (Benson et al. 2010; Tewksbury et al. 1998; 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 (Lahti 2001; Tewksbury et al. 1998). Including predator identity has been recommended when assessing the relationship between habitat and nest predation (Lyons et al. 2015; Phillips et al. 2003; Stephens et al. 2005; Tewksbury et al. 2006), and recent work has shown that this can lead to a better understanding of patterns of nest predation (Benson et al. 2010; Chiavacci et al. 2018; DeGregorio et al. 2016).

When predator identity is known via the use of remote cameras (e.g., Andes et al. 2019; Ellis et al. 2018; McKinnon and Bêty 2009), 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 (Chiavacci et al. 2018; DeGregorio et al. 2016). 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) (Laidlaw et al. 2015; Brown and Litvaitis 1995; 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 (Andres et al. 2012; Studds et al. 2017; Colwell 2010; 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; Ma et al. 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

This study was conducted at two areas in Utah, USA: western Utah, and Great Salt Lake (Fig. 3-1). The western Utah study area included Fish Springs National Wildlife Refuge (2011 – 2017), the United States Army Dugway Proving Ground (2011 – 2017), and Blue Lake (2016 – 2017). Fish Springs National Wildlife Refuge covers 36 km^2 of marsh habitat fed by several thermal springs (Stolley et al. 1999). Spring water flows from Fish Springs National Wildlife Refuge onto the alkaline flats of the United States Army's Dugway Proving Ground, providing approximately 200 km^2 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. In western Utah, the occupancy of snowy plovers is low and associated with scarce 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.

We also collected data along the eastern edge of Great Salt Lake at Saltair (40°46’00” N, 112°09’50” W) and Antelope Island State Park (41°05’08” N, 112°08’08” W) 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 the largest breeding population 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 (Cavitt et al. 2014; Conover 1983) provide multiple challenges to the conservation of snowy plovers and other shorebirds. 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 conducted nest surveys at least once per week at each site during the breeding season (early April – mid August) (Ellis et al. 2015; Paton 1995) to locate new nests and determine the status of extant nests. Once nests were located, we floated eggs to estimate incubation stage and initiation date assuming an egg-laying period of 3 days and a 27-day incubation period (Paton 1995; Page et al. 2009). To determine nest fate and identify predators, we used Reconyx PC900 infrared-triggered cameras (Reconyx, Inc., Holmen, Wisconsin). Cameras were attached to stakes, placed approximately 2 m away from nests, and were elevated 15 – 30 cm above the 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 *Larus* spp., 2) Common Raven *Corvus corax*, 3) coyotes *Canis latrans*, 4) foxes (red foxes *Vulpes vulpes* at Great Salt Lake sites and kit foxes *Vulpes macrotis* at western Utah sites) and 5) other (white-tailed antelope ground squirrels *Ammospermophilus 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 (Conover 2007; Martin et al. 2000b). 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-m^2 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-m^2 area. Snowy plovers often nest in debris or other non-vegetation materials (e.g., cattle dung, carcasses), 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 four spatial scales surrounding nests (200, 500, 1000 and 2500 m buffer sizes) to calculate land cover proportions and density of habitat edges. 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, thus we did not have enough samples to separate intensity of human development. We used the *raster* (Hijmans 2019) and *sp* (Pebesma 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 a nest was active 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 because we were primarily interested in dynamics of nest predation. The model has the form:

$$y_i \sim Multinomial\left(S, P_{j=1}, \cdots, P_{j=J}, 1\right) \tag{1}$$

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

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 four candidate scales for the predictors of landscape characteristics $\boldsymbol{X}^i$ (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 $\boldsymbol{sc}_j$, representing a matrix of seven landscape covariates at four 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 at each scale was moreover estimated by a regression coefficient, contained within the matrix of coefficients for cause of nest predation *j*: $\boldsymbol{\beta}_j$. 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 $\boldsymbol{Z}^{i,t}$, 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 $\boldsymbol{\alpha}_j$. The effects of these predictors on predator-specific hazard rates were collectively modeled through a log-link as:

$$\log(h_j^{i,r,t}) = \boldsymbol{X}^i\, \boldsymbol{\beta}_j\left[\boldsymbol{sc}_j\right] + \boldsymbol{Z}^{i,t}\boldsymbol{\alpha}_j + \varepsilon_j^r + \gamma_j^t,$$

$$\varepsilon_j^r \sim Norm\left(0, \sigma_j^{2,r}\right),\ \gamma_j^t \sim Norm(0, \sigma_j^{2,t}) \qquad (2)$$

where year *r*, and day of season *t* were included as random effects (ε_j^r and γ_j^t, 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 $\sigma_j^{2,r}$ or $\sigma_j^{2,t}$, respectively. Nests 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 $\boldsymbol{\beta}_j$ and $\boldsymbol{\alpha}_j$. We used a categorical distribution for indicators of the candidate scales $\boldsymbol{sc}_j$ with equal prior probabilities that summed to 1 (because we had four candidate scales, each scale had a non-informative prior weight of 0.25). 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). We generated 3 MCMC chains for 200,000 iterations with 20,000 burn-in and 50,000 adaptive iterations, and a thinning rate of 30. We assessed convergence using the Gelman-Rubin diagnostic $\hat{\mathrm{R}}$ (Gelman et al. 2004) and visual inspection of trace plots. Convergence was achieved for estimated parameters (all $\hat{\mathrm{R}} < 1.1$, 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 (s.d. on the link scale = 0.68, 95% BCI = 0.01 – 3.17), compared to 0.42 (95% BCI = 0.02 – 1.42) for ravens, 0.37 (95% BCI = 0.01 – 1.19) for coyotes, and 0.26 (95% BCI = 0.01 – 0.86) 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 the vicinity of nests. At the nest-site, the mean (± standard error, 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 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 3-2). 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 scales (2500 m) for all predator groups with high posterior probabilities (0.97, 0.95, 0.93, and 0.63 for ravens, gulls, coyotes, and foxes, respectively). Similarly, the density of habitat edges was estimated to predict nest predation at 2500 m for ravens, gulls, and coyotes (posterior probabilities: 0.97, 0.80, 0.96, respectively), 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 were most supported at a 500 m scale (posterior probabilities: 0.62, 0.72, and 0.66, 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: 0.79, shrub 2500 m posterior probability: 0.62, shrub 1000 m posterior probability: 0.37). We did not identify a clearly supported spatial scale for the influence of human development on nest predation by coyotes and foxes, however, development influenced predation by gulls at smaller spatial scales (200 m posterior probability: 0.82) and larger scales for ravens (2500 m posterior probability: 0.75). The proportion of water most influenced nest predation by gulls at 500 m (posterior probability: 0.82) 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. 3-3), however the effect of playa on nest predation by foxes was weaker (66% of β_f^{playa} 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 (61% of $\beta_f^{edge} > 0$, 72% of $\beta_r^{edge} > 0$). The remaining land cover types elicited variable responses by nest predators. Nest predation increased with the proportion of grass for foxes (87% of $\beta_f^{grass} > 0$), yet decreased for ravens, gulls, and coyotes (84% of $\beta_r^{grass} < 0$, 96% of $\beta_g^{grass} < 0$, 79% of $\beta_c^{grass} < 0$). Similarly, nest predation by foxes and coyotes increased with proportion of shrubs, and decreased for gulls (90% of posterior distributions on the same side of 0 as the mean). Open water increased nest predation by both avian predators, while human development increased the probability of nest predation by gulls (90% of posterior distributions > 0) but not coyotes, foxes, or ravens as indicated by wide posterior distributions and means centered near 0 (Table 3-1).

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 3-1). Nest predation by ravens and foxes decreased as distance to nearest nest increased (90% of posterior distributions < 0, Table 3-1, Fig. 3-4). 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 3-1).

DISCUSSION

Patterns of predation can be influenced by landscape structure, 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. For example, foxes and ravens are important nest predators for many ground-nesting species (O'Neil et al. 2018; Peterson and Colwell 2014; Draycott et al. 2008; Liebezeit and Zack 2008), yet were influenced by the landscape at different spatial scales. In addition, relationships between land cover characteristics and nest predation by mammalian predators were 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). These differences in predator response 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 (Batary and Baldi 2004; Stephens et al. 2004; Lahti 2001), 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). 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 (Laidlaw et al. 2015; Spautz et al. 2006; Tozer et al. 2010). Wetland habitats are among the most endangered ecosystems worldwide but provision more ecosystem services per unit area than any other type of ecosystem (Zedler and Kercher 2004; 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; Haig et al. 2019; Senner et al.

2018). 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; Lor and Malecki 2006).

The Great Salt Lake was dominated by avian predators, and ravens are often associated with anthropogenic subsidies and water sources (Boarman et al. 2006; Kristan III and Boarman 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 gulls *Larus californicus* in the interior west of North America with many colonies centered around landfills and human developments (Cavitt et al. 2014; Conover 1983). Gull predation can have substantial effects on seabird colonies (Scopel and Diamond 2017, 2018), 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 (Saalfeld et al. 2013; Smith et al. 2007; Liebezeit and Zack 2008; McKinnon and Bêty 2009), 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; Ackerman et al. 2006). 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), but one relevant example includes the use of roads or levees as movement corridors into wetland environments (Frey and Conover 2006). A potential explanation for why we did not detect a relationship between nest predation and the proportion of human development by mammalian predators may be that coyotes and foxes were important nest predators in western Utah where alterations of the landscape by humans is minimal compared to the Great Salt Lake where birds were the dominant predators. 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 often have a high degree of spatial overlap, however kit foxes may 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 dispersal), 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 1,841 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, suggesting 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; Hunt et al. 2018; Ellis et al. 2015). We speculate that at the nest-site scale, predators are also influenced by adult incubation behaviors (Pretelli et al. 2016; 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 predation at multiple landscape scales (Chiavacci et al.

2018). Further, once these predator-specific relationships are assessed, managers could employ structured decision making to identify optimal strategies for reducing nest predation, and continue monitoring nest predators to feed back into the learning process in an adaptive management framework (Walters 1986). 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.

Table 3-1. Posterior estimates of coefficients for nest-site variables which estimated predator-specific hazard rates of nest mortality. Bold entries represent estimates with 90% of the posterior distribution on the same side of 0 as the mean.

Variable	Mean estimate	2.50%	97.50%
Coyote			
Bare ground	-0.25	-0.68	0.17
Nearest nest	-0.07	-0.51	0.32
Robel obscurity	-0.31	-0.77	0.13
Fox			
Bare ground	0.08	-0.22	0.38
Nearest nest	-0.93	-1.54	-0.42
Robel obscurity	0.40	0.12	0.67
Gull			
Bare ground	0.41	0.05	0.79
Nearest nest	-0.15	-0.48	0.14
Robel obscurity	-0.46	-0.79	-0.13
Raven			
Bare ground	-0.02	-0.33	0.28
Nearest nest	-1.15	-1.77	-0.61
Robel obscurity	0.32	-0.02	0.64

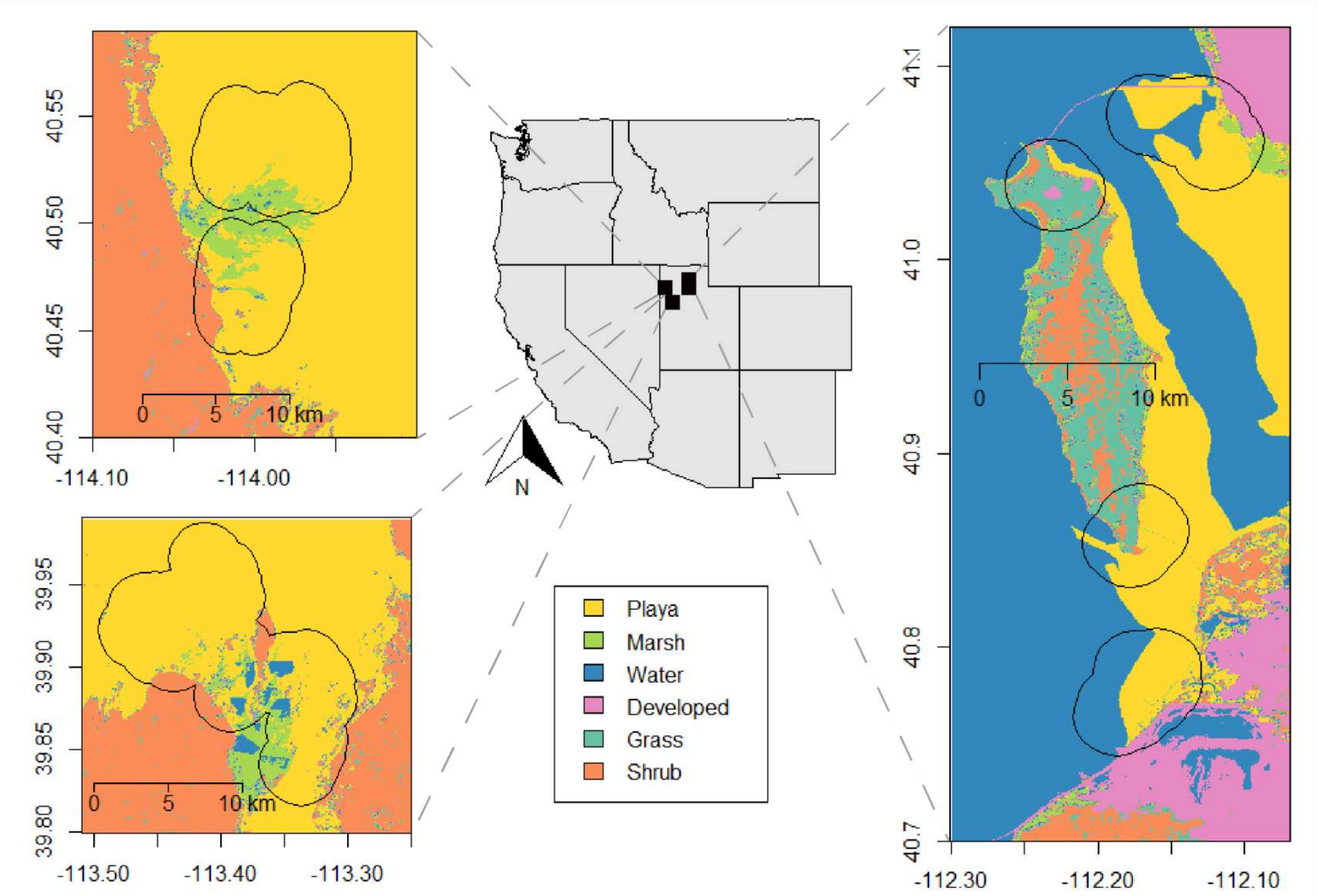

Figure 3-1. Location of study areas in Utah, USA including the Great Salt Lake (right) and western Utah (Blue Lake top left, Fish Springs National Wildlife Refuge and Dugway Proving Ground bottom left). Black outlines represent 2500 m buffers surrounding

nests. Landscape metrics were measured in 4 different-sized and concentric buffers from the center of each nest (250, 500, 1000, and 2500 m).

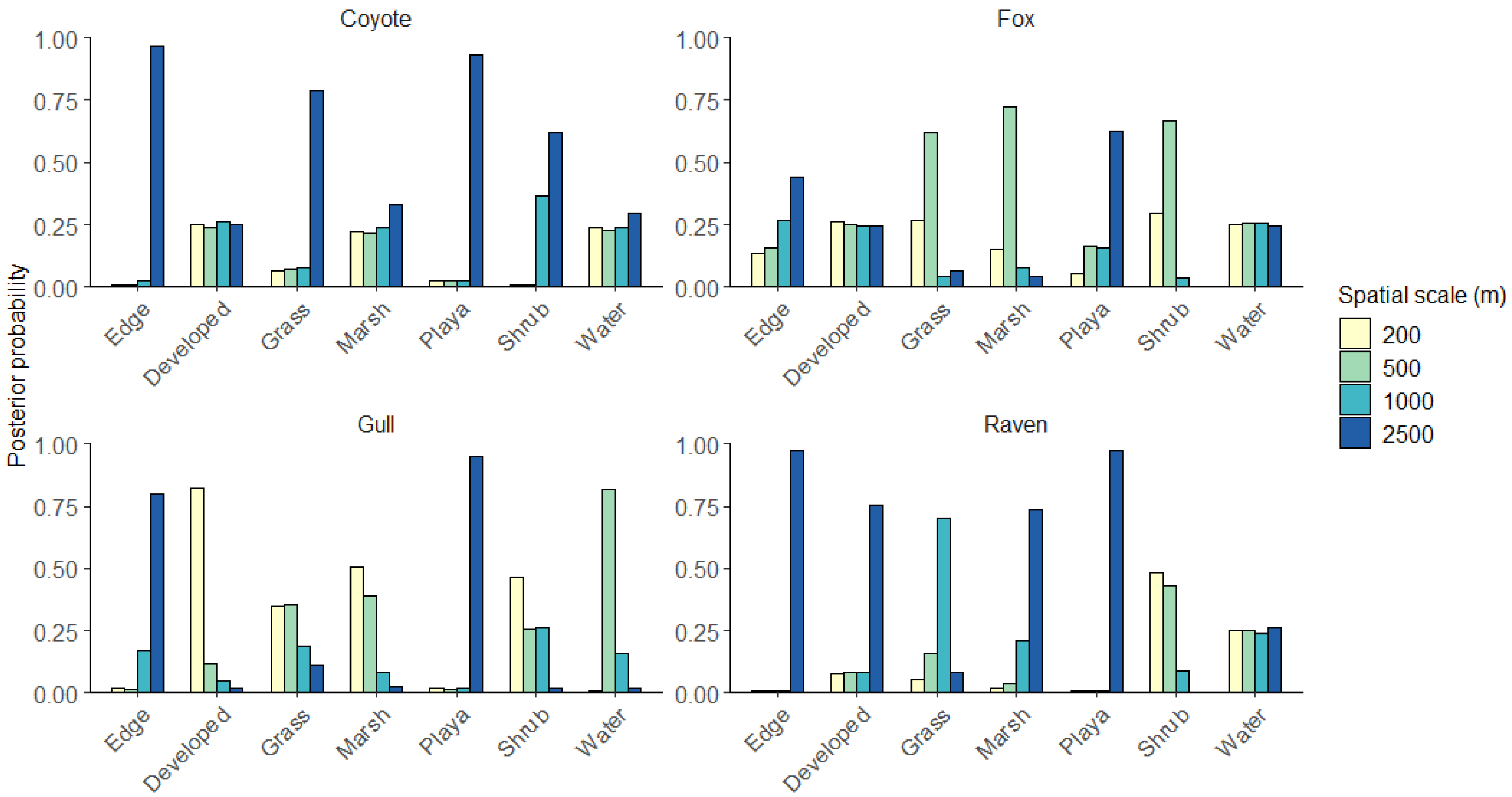

Figure 3-2. Posterior distributions of support for the spatial scales at which land cover predictors most affect nest predation by specific predators for density of habitat edge, and proportions of human development, grass, marsh, playa, shrub, and open water surrounding snowy plover nests.

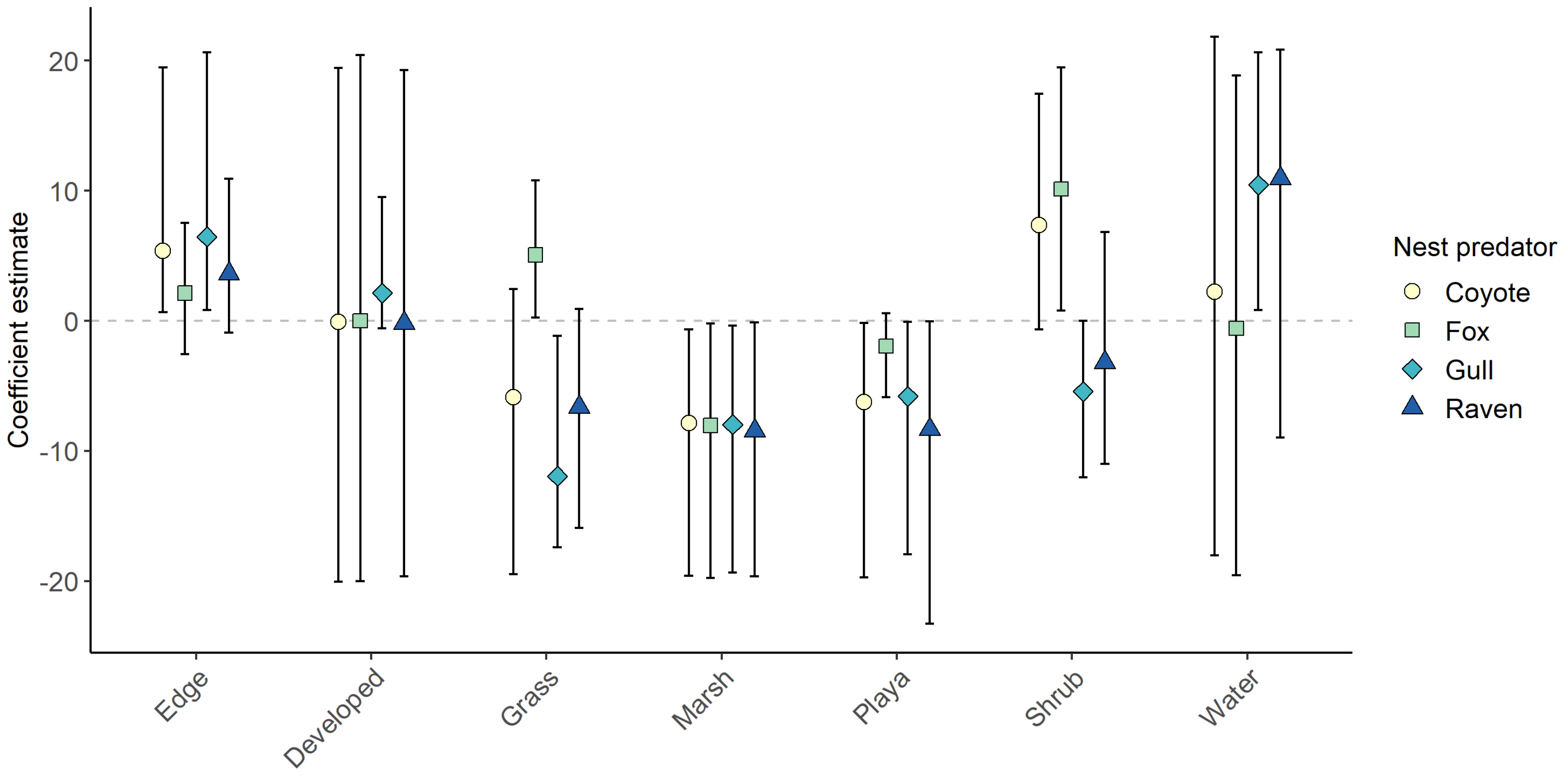

Figure 3-3. Estimated means and 95% Bayesian credible intervals of land cover parameters explaining relationships between density of habitat edges, and proportions of human development, grass, marsh, playa, shrub, and open water within 200, 500, 1000, and 2500 m of nests and hazard rates of nest mortality by coyotes, foxes, gulls, and ravens in Utah, USA 2011 – 2017. Estimates are weighted averages across candidate spatial scales and the model also included study area (Great Salt Lake or Western Utah), nest-site characteristics, and distance to nearest nest.

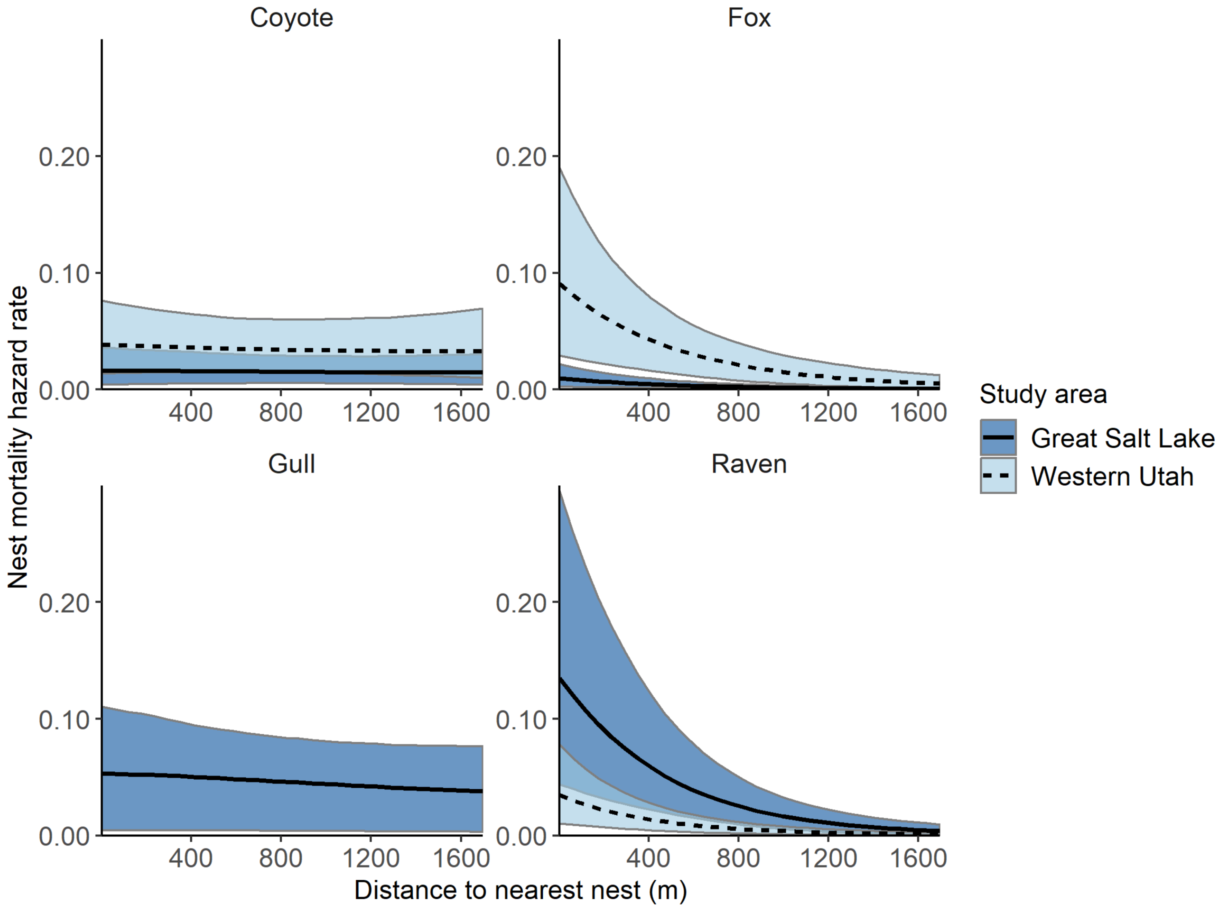

Figure 3-4. Predicted probabilities of nest predation by specific predators with increasing distance to nearest nest (note that gulls were not a source of nest mortality in western Utah). Mean predictions (black lines) and 95% Bayesian credible intervals (shaded areas) are shown for each study area.

CHAPTER 4: PLASTICITY OF SNOWY PLOVER INCUBATION BEHAVIOR IN RESPONSE TO PREDATOR-SPECIFIC RISKS OF NEST PREDATION

SUMMARY

Characterizing variation in parental care in response to fluctuating environmental conditions can lead to a better understanding of how individuals balance trade-offs between the needs of their offspring and themselves. Nest predation is an important driver of avian life history evolution and population dynamics, and increasing evidence indicates that breeding birds can assess the risks of nest predation and adjust their strategies of parental care. Because adult behaviors during incubation can provide cues to nest predators, we would predict that incubating birds would decrease conspicuous behaviors at the nest-site, and increase incubation constancy (to allow for nest-defense behaviors) when risks of nest predation are high. We examined whether breeding pairs of snowy plovers *Charadrius nivosus* perceived, and responded to predator-specific risks of nest predation, using the number of off-bouts and proportion of nest attendance as responses. To represent these risks, we used predator-specific hazard rates of nest mortality, which varied daily and were based on habitat characteristics at each nest. We used Bayesian mixed-effect models (Poisson distribution for number of off-bouts and beta distribution for nest attendance) to examine the influence of predator-specific risks of nest mortality on incubation behaviors, which allowed us to incorporate uncertainty around hazard rate predictors. For both metrics of incubation behavior that we considered as response variables, we noted an increase in parental care in response to increasing risks of nest predation by foxes (*Vulpes* spp.) and gulls (*Larus* spp.), but not coyotes (*Canis latrans*) and common ravens (*Corvus corax*), within breeding pairs. Between breeding pairs, we similarly noted an increase in parental care in

response to increasing risks of nest predation by foxes, but not coyotes, gulls, or ravens. Further, breeding pairs differed in the amount of behavioral plasticity they exhibited in response to risks of nest predation. Our results suggest that risks of nest predation differentially influence behavioral responses by snowy plovers depending on the predator species, and that the amount of plasticity may depend on individual characteristics of breeding adults.

INTRODUCTION

Parental care strategies are predicted to balance the fitness costs and benefits associated with providing care to offspring (Clutton-Brock 1991; Stearns 1992). Yet in dynamic environments, behavioral plasticity may confer the greatest fitness benefits such that no fixed amount or type of parental care is reliably optimal among individuals, populations, or species (Royle et al. 2014). The risk of predation is an environmental factor that varies spatially and temporally, and can alter many aspects of behavioral and reproductive decision-making (Lima and Dill 1990; Lima 2009). Thus, plasticity in behavioral responses that track risks of predation should lead to fitness benefits. Variation in avian responses to nest predation suggests that many reproductive strategies appear to reflect the importance of nest predation as a selective force (Martin 1995; Lima 2009; Newton 1998). Yet even the perceived risk of nest predation has resulted in a suite of adaptations (reviewed in Lima 2009). These adaptations may include reductions in reproductive effort when the risk of nest predation is high (Zanette et al. 2011; van Kleef et al. 2007; Eggers et al. 2006), changing nest-site location at small scales (Eggers et al. 2006; Peluc et al. 2008; Forstmeier and Weiss 2004; Amat and Masero 2004b) or large scales (Lloyd et al. 2005; Fontaine and Martin 2006a), and long-lived species may forgo breeding completely during high-risk seasons (Quakenbush et al. 2004; Spaans et al. 1998). For species where one mate provides food to the incubating parent, provisioning rates decrease or are suspended when parents face an increased risk of nest predation (Ghalambor and Martin 2002; Ghalambor et al. 2013; Martin et al. 2000a). But for species without mate provisioning, risks of nest predation can also lead to overall minimized activity at the nest (Massaro et al. 2008; Basso and Richner 2015; Smith et al. 2007). While reducing predation risk to the nest through behavioral changes in incubation may increase the probability of nest success (Smith et al. 2007), these behavioral changes may result in decreased resources available for future survival and fecundity of the incubating adult.

Whereas more conspicuous behaviors by parents at the nest may increase the risk of nest predation by providing cues to visual predators (Smith et al. 2012; Cresswell et al. 2003). However, birds must manage trade-offs between current reproduction and self-maintenance during incubation. Certain plover species (*Charadrius* spp.) cope with hot mid-day temperatures by increasing biparental cooperation and limiting the length of incubation bouts by each parent (Amat and Masero 2004a; AlRashidi et al. 2010b; Vincze et al. 2016; Vincze et al. 2013). These more frequent on- and off- bouts to minimize costs to individuals may nevertheless result in greater rates of nest predation due to additional visual cues. Red-capped plovers (*Charadrius ruficapillus*) are biparental incubators and sexually dichromatic, and will adapt incubation schedules to be consistent with activity patterns of visual predators, whereby more colorful males incubate at night (Ekanayake et al. 2015). Consequently, incubation strategies are predicted to vary as a function of energetic needs, ambient weather conditions, and predator pressure (Norton 1972; Bulla et al. 2014; Tulp and Schekkerman 2006; Bulla et al. 2015).

The non-lethal effects of increased risks of nest predation may be a consequence of reduced foraging opportunities, when incubating birds invest more energy in their offspring (Cresswell 2008). While incubation is energetically demanding (Tinbergen and Williams 2002), experimental evidence in biparental shorebirds breeding in the Arctic indicated that incubation scheduling was not primarily driven by energetic constraints alone (Bulla et al. 2015). Thus, the trade-off between self-maintenance and current offspring is likely dynamic with variation in risks of nest predation, and even more so when multiple predator species are present in the community that may impose different risk levels (Basso and Richner 2015). Incubating birds may perceive risks differently based on predator foraging strategies (e.g., diurnal or nocturnal) and target prey (adults and clutch compared to only the clutch; Basso and Richner 2015; Ghalambor and Martin 2001). But effects of specific predators on incubation strategies in birds are still poorly understood, particularly for species that exhibit biparental incubation.

Our objective was to assess how spatial and temporal variation in predator-specific risks of nest predation influence incubation behaviors in snowy plovers (*Charadrius nivosus*). Snowy plovers are vulnerable to a suite of avian and mammalian nest predators across their range (Ellis et al. 2018), which may impose risks differentially based on foraging strategies (avian predators use visual cues during flight diurnally, whereas mammalian predators use systematic searches and olfactory cues nocturnally or crepuscular periods). We predicted that incubating adults will exhibit less conspicuous incubation behaviors when the risk of nest predation is high, specifically by visual predators. Patterns of parental care can vary within individuals through time, known as phenotypic plasticity, but average behaviors and the degree of behavioral plasticity can also vary among individuals with different genotypes in a population (Royle et al. 2014). Thus, to evaluate the effects of risks of nest predation on incubation behaviors at both between-nest and within-nest levels, we used an individual centering approach (Dingemanse and Dochtermann 2013; van de Pol and Wright 2009). Individual centering is useful for distinguishing among- versus within-individual effects by fitting an individual mean effect and its deviation from the mean for each observation. In our case, we used nests as individuals because we could not distinguish between incubating males and females. We therefore treat parental pairs as a ‘genotypic unit’ that can collectively influence offspring fitness via investments in parental care. Our findings provide needed insight into the plasticity of parental behaviors in response to predator-specific risks to offspring in natural conditions, and how nest predation risks may modify trade-offs between current and future reproduction.

METHODS

Study Areas and Data Collection

Our study was conducted at two areas in Utah, USA between 2011 and 2017: western Utah, and Great Salt Lake. The western Utah study area included Fish Springs National Wildlife Refuge (39°51’01” N, 113°23’45” W; 2011 – 2017), the United States Army Dugway Proving Ground (39°56’14” N, 113°25’20” W; 2011 – 2017), and Blue Lake (40°30’11” N, 114°00’55” W; 2016 – 2017). Great Salt Lake sites included Saltair (40°46’00” N, 112°09’50” W) and Antelope Island State Park (41°05’08” N, 112°08’08” W) between 2014 and 2017.

We conducted nest surveys at least once per week at each site during the breeding season (early April – mid August) (Ellis et al. 2015; Paton 1995) to locate new nests and determine the status of extant nests. Once nests were located, we floated eggs to estimate incubation stage and initiation date assuming an egg-laying period of 3 days and a 27-day incubation period (Paton 1995; Page et al. 2009). To measure incubation behaviors, we used photos from Reconyx PC900 infrared-triggered cameras (Reconyx, Inc., Holmen, Wisconsin). Cameras were attached to stakes, placed approximately 2 m away from nests, and were elevated 15 – 30 cm above the 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. Of critical importance, previous work suggests that cameras do not impact nest survival for snowy plovers (Ellis et al. 2018). We did not place cameras at nests until the laying phase was complete to limit disturbance and avoid nest abandonment, thus no photos used in our analyses included incubation behaviors during the laying phase. Snowy plovers nest in sparsely-vegetated scrapes and because of this open habitat, cameras were able to consistently detect on- and off- bouts by incubating adults. Using photos from nest cameras, we considered two measures of incubation behavior as response variables: nest attendance (proportion of time spent incubating) and number of off-bouts, both within 24-hour periods. 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. Further, we removed any 24-hour period where we could not consistently detect on- and off- bouts due to camera angle, sun glare, or other abnormalities. We excluded the first day cameras were deployed and days where the nests were checked by observers to minimize confounding effects in the analysis, which resulted in 4118, 24-hour periods from 194 nests at Great Salt Lake and 279 nests in western Utah.

Analysis

Estimated Risks of Nest Predation

To measure the risks of nest predation which were used as predictor variables, we estimated predator-specific hazard rates for nest mortality that varied temporally and spatially. Hazard rates can adequately represent the risk of nest predation because they measure the instantaneous probability of mortality occurring per unit time (Heisey and Patterson 2006). We used images from nest cameras to determine nest fate and identify nest predators, the latter of which we categorized into five groups: 1) gulls *Larus* spp., 2) Common Raven *Corvus corax*, 3) coyotes *Canis latrans*, 4) foxes (red foxes *Vulpes vulpes* at Great Salt Lake sites and kit foxes *Vulpes macrotis* at western Utah sites) and 5) other (white-tailed antelope ground squirrels *Ammospermophilus leucurus*, unidentified mice, Northern Harriers *Circus cyaneus*, and raccoons *Procyon lotor*). As described in Chapter 3 in more detail (from which the results are used here), we used a cause-specific hazard model to estimate multiple sources of nest mortality, resulting in predator-specific hazard rates at daily intervals (Heisey and Patterson 2006; Heisey et al. 2007). Because 'other' predators were relatively rare, we treated this group as an intercept only and modeled cause-specific hazard rates with spatial and temporal variables for the other four predator groups: gulls, ravens, coyotes, and foxes. We incorporated spatial covariates so that predator-specific hazard rates reflected nest-specific characteristics, because variation in the landscape and nest-site characteristics may also influence incubation behaviors (AlRashidi et al. 2011). Spatial covariates included in estimating predator-specific hazard rates were 7 landscape covariates (proportions of grasses, open water, playa, shrubs, emergent marsh, and human development), 3 nest-site covariates (percent bare ground within 1-m^2 of the nest, Robel pole obscurity (Robel et al. 1970), and distance to nearest nest on each day of the breeding season. Because 'estimated' hazard rates from another analysis were used as predictor variables for incubation behaviors, we accounted for the uncertainty in these predictors using a two-level analysis whereby the standard deviation around hazard estimates were used to derive entire distributions for each level of a hazard predictor, rather than the improper practice of conducting statistics on just the statistical means while disregarding any uncertainty in a predictor.

Incubation Behavior Models

To evaluate how risks of nest predation influence two measures of snowy plover incubation behavior, we used mixed-effect models and predictor variables included predator-specific hazard rates representing risks for locations of each nest on each day of the breeding season. Nest attendance was measured as a proportion (between 0 and 1), which requires a probability model restricted to this interval for analysis. The beta distribution provides a flexible parametric model that can be used to analyze proportional data and does not assume constant variance across the response variable, unlike normal linear models with transformed proportional data (Douma and Weedon 2019). Following the approach to beta regression developed by Ferrari & Cribari-Neto (2004), our model for nest attendance took the following form:

$$y_{i,j} \sim Beta\left(\mu_{i,j}\phi, \phi\left(1-\mu_{i,j}\right)\right) \tag{1}$$

where the $y_{i,j}$ are observed proportions of nest attendance for nest j on day i. We estimated ϕ (the spread parameter in the beta distribution) as a single value for all observations, rather than modeling it as a function of covariates, after calculating standardized residuals (Espinheira et al. 2008) and not detecting any patterns when visually compared with predicted values (Douma and Weedon 2019). The $\mu_{i,j}$ represents the mean response for nest attendance and was modeled using a logit link: $logit\left(\mu_{i,j}\right) = \eta$, where η is a linear predictor. Alternatively, the number of off-bouts by incubating adults was modeled using a Poisson probability distribution with a log link: $log\left(\lambda_{i,j}\right) = \eta$, where $\lambda_{i,j}$ represents the mean response and η is a linear predictor.

We used mixed-effect models with nest-centered predictor variables (Dingemanse and Dochtermann 2013; van de Pol and Wright 2009) for explaining within (plasticity) and among individual variation in the two measures of incubation behavior, where the linear predictor was:

$$\eta_{i,j} = (B_0 + \gamma_{0j}) + (B_W + \gamma_{Wj})\left(R_{i,j} - \bar{R}_j\right) + B_B\bar{R}_j + B_T T_{i,j} + B_I I_{i,j} + \omega_{y,j} + \varepsilon_{i,j} \tag{2}$$

for nest *j* on day i. The overall mean response is given by B_0 and slopes for the relationships between predictors and behavioral response were B_W (within-nest), B_B (between-nest), B_T (temperature), and B_I (incubation date). $R_{i,j}$ indicates an 'uncertain' covariate for daily predator-specific hazard rates of nest mortality, $\overline{R}_j$ indicates the temporal mean of each predator-specific hazard rate each nest experienced (with uncertainty), $T_{i,j}$ indicates the mean daily temperature, and $I_{i,j}$ indicates day of incubation (nest age). Random intercepts for individual nests were represented by γ_{0j} along with the residual error term $\varepsilon_{i,j}$, which were each assumed to be drawn from a normal distribution with zero mean and between-subject variance $\sigma^2_{\gamma 0,j}$ and within-subject variance $\sigma^2_{\varepsilon,j}$, respectively. Year *y* was similarly included as a random intercept, represented by $\omega_{y,j}$ and was drawn from a normal distribution with zero mean and variance $\sigma^2_{y,j}$. We included random slopes γ_{Wj} for the within-nest effect so we could quantify the amount of between-nest variation in within-nest slopes around B_W, where γ_{Wj} was drawn from a normal distribution with zero mean and between-nest variance $\sigma^2_{\gamma W,j}$ (Dingemanse and Dochtermann 2013). These later effects are especially important for making inference about phenotypic plasticity in parental care behavior. We ran separate models for each predator group because their hazard rates were correlated (Chapter 2) and may have caused issues with multicollinearity if combined into a single model. Thus, we modeled estimates of risks of nest predation from four predator groups and two response variables (nest attendance and number of off-bouts), resulting in 8 total models. We evaluated the degree of correlation between intercepts and slopes of individual nests using the *cor* function in R (R Development Core Team 2018). We used correlations to measure variation in plasticity in behavioral responses to mean risks of nest predation among individual nests. Specifically, we calculated Pearson's correlations between

Markov chain Monte Carlo (MCMC) samples for every combination of γ_{Wj} and γ_{0j} to derive posterior distributions of correlated relationships.

Estimation

Parameters in the mixed-effect models were estimated using a Bayesian application of MCMC sampling in JAGS (Plummer 2017), and cast in R via the package *jagsUI* (Kellner 2018). We chose vague priors for all parameters including a uniform [0, 10] distribution for hyperpriors on random-effect standard deviations. In Poisson regression models (for number of off-bouts), we used a normal distribution with mean 0 and standard deviation of 10 for intercept and coefficient priors. In beta regression models (for nest attendance), we used a logistic distribution with α centered at 0 with scale parameter 1 for intercept and coefficient priors, which is a suitable vague prior distribution when using a logit link (Northrup and Gerber 2018; Dorazio 2016). We generated three MCMC chains and assessed convergence using the Gelman-Rubin diagnostic $\widehat{\mathrm{R}}$ (Gelman et al. 2004) and visual inspection of trace plots. We ran models for 50000 iterations, with an adapt phase of 10000, burn-in of 10000, and thinning rate of 20. For all models, convergence was achieved for estimated parameters (all $\widehat{\mathrm{R}} < 1.1$, with trace plots showing mixing among stationary MCMC chains). We scored the predictive ability of models relative to one another using WAIC (Watanabe 2010) by monitoring log-likelihoods for the y_i and then applying the *waic* function in the *loo* package for R (Vehtari et al. 2018).

RESULTS

The mean daily nest attendance (proportion of time spent incubating) by snowy plovers was 0.90 (s.d. = 0.04), but also exhibited considerable variation (range = 0.71 – 0.99) among and within individuals. The mean number of off bouts taken by snowy plovers in a 24-hour period was 22.59 (s.d. = 11.54), which also exhibited considerable variation (range = 11 – 67) among and within individuals. Both nest attendance and number of off bouts increased with mean daily temperatures (Table 4-1). Nest attendance increased with nest age (as nests approached hatching date), but nest age did not influence the number of off bouts.

Among models of daily nest attendance, the risk of nest predation by gulls provided the best model fit, relative to foxes (ΔWAIC = 95.52), coyotes (ΔWAIC = 143.62), and ravens (ΔWAIC = 241.92; Table 4-1). Within nests, nest attendance increased with the risk of nest predation by gulls and foxes (100% and 97% of B_W posterior distributions were > 0, respectively), and the slope of this effect was 5 times greater for gulls than foxes (Table 4-1, Fig. 4-1). Risks of nest predation by coyotes and ravens did not strongly influence nest attendance (within nests), as indicated by B_W posterior distributions centered near 0. Between nests and their associated habitat locations, nest attendance increased with risks of nest predation by foxes (93% of B_B posterior distribution was > 0), yet decreased with risks of nest predation by ravens (99% of B_B posterior distribution was < 0), while the magnitudes of these effects were similar (Fig. 4-2, Table 4-1). Risks of nest predation by coyotes and gulls did not strongly influence nest attendance between nests, as indicated by wide B_B posterior distributions centered near 0.

For the number of off-bouts, WAIC scores were closer among separate models where the risk of nest predation by foxes had the best fit relative to gulls (ΔWAIC = 2.33), ravens (ΔWAIC = 11.82), and coyotes (ΔWAIC = 13.09; Table 4-1). The risk of nest predation by foxes was related to a decrease in the number of off-bouts both within and between nests (99% of B_W and B_B posterior distributions were < 0; Table 4-1, Fig. 4-1, Fig. 4-2). The risk of nest predation by gulls was related to a decrease in the number of off-bouts within nests (97% of B_W posterior distribution was < 0), but not between nests. Risks of nest predation by coyotes and ravens were not influential on the number of off-bouts by snowy plovers, as posterior distributions for both B_W and B_B were wide and centered near 0.

Within individual nests, slopes and intercepts for effects of risks of nest predation by foxes and gulls were negatively correlated for both nest attendance and number of off-bouts (Table 4-1). Nesting pairs that had lower nest attendance when risks of nest predation by foxes and gulls were low, increased attendance at a higher rate (greater plasticity) compared to pairs that had higher nest attendance when risks were low (100% of both posterior distributions were < 0; Fig. 4-1). Alternatively, nesting pairs that had more off-bouts in a 24-hour period when risks of nest predation by foxes and gulls were low, decreased the number of off-bouts at a higher rate than pairs that took less breaks from incubation when risks were low (100% of both posterior distributions were < 0). The correlation between intercepts and slopes was slightly negative for effects of the risk of nest predation by ravens on nest attendance and number of off-bouts (89% and 87% of posterior distributions were < 0, respectively; Table 4-1). Intercepts and slopes for the effects of risk of nest predation of coyotes were not correlated for either behavioral response as indicated by posterior distributions centered near 0 (Table 4-1).

DISCUSSION

Parental care is highly variable within and between individuals in a population (Royle et al. 2014; Westneat et al. 2011), and few studies have explored the role of variation in incubation behavior within breeding pairs in response to risks of nest predation from different predators. Here we applied an individual-centering approach to determine how predator-specific risks of nest predation shape patterns of incubation behavior plasticity within breeding pairs and across individuals in a population of snowy plovers. For both metrics of incubation behavior that we considered as response variables, breeding pairs increased parental care in response to increasing risks of nest predation by foxes and gulls, but not coyotes and ravens (within individual nests). Between nests, we similarly noted an increase in parental care in response to increasing risks of nest predation by foxes, but not coyotes, gulls, or ravens. Interestingly, nest attendance decreased between nests in response to increasing risk of nest predation by ravens. These findings support the growing body of evidence that risks of nest predation can lead to altered behaviors during the nesting period, although much of this work has been conducted on passerine species and using artificial experiments (e.g., Dorset et al. 2017; Ghalambor et al. 2013; Yoon et al. 2016; Behrens et al. 2019; Ghalambor and Martin 2002; Conway and Martin 2000; Fontaine and Martin 2006b). Our findings suggest that behavioral plasticity in response to varying environmental conditions may confer benefits to snowy plovers balancing offspring care and energetic demands of reproduction.

Shorebirds offer an ideal system to examine patterns of parental care because of the substantial variability within and among species (Székely 2019; Bulla et al. 2016). Studies on incubation behavior within shorebird species have previously shown that behaviors vary with temperature and temperature stochasticity (Vincze et al. 2016; Vincze et al. 2013; AlRashidi et al. 2010a), nest-site characteristics (AlRashidi et al. 2011), and day of incubation (Vincze et al. 2013; Bulla et al. 2014), yet unexplained variation among populations may be related to the local risks of nest predation rather than energetic constraints (Bulla et al. 2016). Contrary to our findings, biparental shorebirds have previously been shown to increase the duration of incubation bouts in response to incubation date (Bulla et al. 2014), but not overall nest attendance (Vincze et al. 2013; Bulla et al. 2014). These differences among populations and species suggests that dynamic environmental conditions such as risks of nest predation, distance to foraging locations, and resource availability may modify the plasticity of parental behaviors. Undoubtedly, incubation behavior is dependent on ambient temperature because embryonic development requires a narrow temperature range (Webb 1987). Flexible incubation behaviors may thus alleviate effects of warming temperatures associated with climate change in species with biparental incubation through increased contribution from males (Vincze et al. 2016). However, in species with sexually dimorphic coloration, nest predation may limit the benefits of male care during the day because of their brighter plumage, which may make them easier to detect by visual predators (Ekanayake et al. 2015).

We found that snowy plovers took fewer off-bouts when risks of nest predation by gulls was high, but not ravens, which partially supports our prediction that incubating pairs would exhibit less conspicuous behaviors when risks of nest predation by visual predators was high. Skutch (1949) first proposed the relationship between frequent trips to and from the nest (to feed altricial nestlings) and increased nest predation by predators that use visual cues. Indeed, it has been shown that the number of off-bouts is related to increased nest predation during incubation (Smith et al. 2012) and the nestling period in species with altricial offspring (Martin et al. 2000b; Martin and Ghalambor 1999), although there may be instances where this relationship is not supported (e.g., when dominant nest predators are nocturnal) (Roper and Goldstein 1997). Further, increased nest attendance may decrease nest predation because breeding adults will be present to perform defense behaviors when predators approach (e.g., distraction displays; Gochfeld 1984). Because incubation behaviors can influence the probability of nest success, there should be fitness benefits to identifying predator cues and adjusting behaviors. A potential explanation for why we observed predicted responses (reduced number of off-bouts and increased nest attendance) with increased risks of nest predation by gulls but not ravens may be due to differences in foraging behaviors of these nest predators. California and ring-billed gulls

(*Larus californicus* and *L. delawarensis*), both common nest predators in our study, are among the most abundant avian species at the Great Salt Lake and typically forage in large groups (Cavitt et al. 2014; Baird 1976). This colonial behavior, coupled with vocalizations during flight (Nelson and Baird 2001), may have provided consistent cues to snowy plovers when risks of nest predation by gulls were high. Comparatively, raven abundance is lower in playas and salt flats compared to other habitats and ravens typically forage in small groups or solitarily (Webb et al. 2009). These less-visible foraging cues may have contributed to why we did not detect a change in the number of off-bouts or nest attendance by snowy plovers in response to risks of nest predation by ravens. Yet we did observe reduced off-bout frequency and increased nest attendance with increasing risks of nest predation by foxes, suggesting that there may be cues of cryptic mammalian predators that birds can detect, which is consistent with patterns observed in nesting ducks and their meso-carnivore nest predators (Dassow et al. 2012).

Our results indicated that breeding pairs varied in their behavioral slopes and mean responses to risks of nest predation by foxes and gulls, revealing that breeding pairs may differ in the amount of behavioral plasticity they exhibit (i.e., varying personalities between breeding pairs; Dingemanse et al. 2010). Because nesting is energetically costly to breeding adults (Tinbergen and Williams 2002), those that displayed relatively more parental care when risks of nest predation were low may have been energetically constrained such that the amount of parental care could not increase at the same rate as those that displayed lower parental care. Yet breeding pairs that displayed more behavioral plasticity (relatively less parental care) when risks of nest predation were low could have benefited from increased foraging opportunities. Differences in parental state (such as age or body condition) could influence the trade-offs of parental care, which could favor different behavioral strategies between individuals (Dingemanse et al. 2010). For example, older individuals may invest more time incubating their current clutch at the expense of future survival and mating opportunities (Yerkes 1998), and long-lived birds in poor body condition may decrease parental care and favor future survival and mating opportunities (Criscuolo et al. 2002). Thus, incorporating parental state in future research may lead to a better understanding of why certain breeding pairs exhibited more behavioral plasticity in response to risks of nest predation.

Nest predators may impose different risks based on hunting strategy or target prey (only eggs or adults and eggs). Consequently, responses by incubating birds should reflect the type of risks they encounter (Curio et al. 1983; Ghalambor and Martin 2001; Basso and Richner 2015). For example, some species may use different alarm calls depending on predator size and type (Curio et al. 1983; Templeton et al. 2005). When predators target both adults and eggs, adults must risk either their offspring or themselves, and predictions of this decision depend on life-history characteristics of the species (Ghalambor and Martin 2001). Because snowy plovers can have multiple, small clutches (average 3 eggs) in a single breeding season, and have relatively high adult survival rates (apparent adult survival at our study area estimated at 0.687; Paton 1994), we might predict that adults would reduce parental care when the risk of predation to themselves is high. Although behavioral responses varied with specific predators, our results did not reveal consistent patterns between predators that may have targeted incubating adults as well as eggs (coyotes and foxes) compared to predators that targeted only eggs (gulls and ravens). Clearer patterns may have emerged if we had used predator-specific experimental treatments rather than hazard rates of ‘nest mortality’ which may not necessarily capture risks to incubating adults.

A benefit to our approach of using nest- and daily-specific hazard rates of nest mortality as predictors of incubation behavior is that we do not fully understand what cues incubating birds use to assess predator risk, and experimentally simulated risks may not be perceived as such (Stelbrink et al. 2019). While visual and auditory cues have been experimentally shown to induce behavioral changes (Ghalambor and Martin 2001; Ghalambor and Martin 2002; Peluc et al. 2008); but see (Stelbrink et al. 2019)), we do not fully understand how incubating birds detect risks by cryptic predators, such as kit foxes. Our results indicate that incubating snowy plovers either respond differently to risks presented by specific predators, or differ in their ability to perceive cues by specific predators. However, we did note substantial behavioral changes (e.g., a 70% decrease in the number of off-bouts within breeding pairs in response to increasing risks of nest predation by foxes), which may be associated with non-lethal effects of predation. Perhaps the most obvious non-lethal effect from changes in incubation in response to risks of nest predation is changes in foraging opportunities, which has implications for body condition and survival (Cresswell 2008). However, many species respond to predation risk with altered stress hormones, metabolic rates, and gene expression (Sheriff and Thaler 2014; Zanette et al. 2014). The indirect effects of predation risk on prey population dynamics can be as large or larger than the effects from direct predation (Nelson et al. 2004; Preisser et al. 2005). Thus, evaluating the plasticity and heterogeneity of behaviors in response to specific risks of predation may allow us to better understand the mechanisms underlying how predators alter prey populations.

Table 4-1. Posterior parameter estimates from mixed models that use within-nest centering (Eqn. 2) to evaluate snowy plover incubation behaviors in response to predator-specific hazard rates of nest mortality, while accounting for temperature, nest age, and annual effects. We present mean estimates with 95% Bayesian credible intervals. Bold entries represent effects for the risks of nest predation covariates only (B_W and B_B), or correlations between slopes and intercepts for individual nests (r), where 90% of the posterior distribution was on the same side of 0 as the mean.

Model parameter	Fox	Coyote	Raven	Gull
Nest attendance (Beta distribution with logit link)				
ϕ	100.97 (96.86, 105.10)	100.86 (96.71, 104.94)	101.11 (96.94, 105.42)	102.79 (98.53, 106.98)
B_0	2.05 (1.96, 2.14)	2.07 (1.99, 2.16)	2.07 (1.98, 2.17)	2.06 (1.97, 2.14)
B_W (within nests)	**0.92 (-0.03, 1.86)**	0.54 (-2.69, 3.68)	0.08 (-0.37, 0.59)	**5.03 (3.91, 6.17)**
B_B (between nests)	0.62 (-0.23, 1.48)	-1.34 (-4.44, 1.23)	**-0.77 (-1.37, -0.15)**	-0.11 (-2.11, 1.91)
B_T (mean temperature)	0.14 (0.13, 0.15)	0.14 (0.13, 0.15)	0.14 (0.13, 0.15)	0.14 (0.13, 0.15)
B_I (incubation date)	0.01 (0.001, 0.02)	0.01 (0.001, 0.02)	0.01 (0.001, 0.02)	0.01 (0.001, 0.02)
σ_B^2 (between nest variance in intercept)	0.11 (0.10, 0.13)	0.12 (0.10, 0.13)	0.11 (0.10, 0.13)	0.11 (0.10, 0.13)
σ_W^2 (residual variance)	0.20 (0.17, 0.23)	0.18 (0.15, 0.21)	0.21 (0.19, 0.24)	0.20 (0.18, 0.23)
σ_y^2 (annual variance)	5.05 (0.23, 9.75)	4.95 (0.25, 9.76)	4.98 (0.28, 9.75)	5.04 (0.27, 9.78)
$\sigma_{\gamma W}^2$ (between nest variance in slope)	3.37 (1.93, 5.15)	9.70 (8.86, 9.99)	0.52 (0.02, 1.68)	3.41 (0.93, 5.42)
r (intercept/slope)	**-0.58 (-0.70, -0.45)**	0.00 (-0.12, 0.13)	-0.16 (-0.39, 0.08)	**-0.69 (-0.79, -0.59)**
WAIC	-21355.18	-21307.08	-21208.78	-21450.70
Number of off bouts (Poisson distribution with log link)				
B_0	3.08 (2.84, 3.32)	3.08 (2.83, 3.32)	3.05 (2.81, 3.28)	3.03 (2.78, 3.28)
B_W (within nests)	**-1.00 (-1.63, -0.35)**	3.02 (-2.91, 7.37)	-0.18 (-0.87, 0.49)	**-0.99 (-2.10, 0.06)**
B_B (between nests)	**-1.92 (-3.43, -0.32)**	-4.41 (-11.40, 7.01)	0.22 (-1.07, 1.49)	1.50 (-4.12, 6.69)
B_T (mean temperature)	0.07 (0.05, 0.08)	0.06 (0.05, 0.08)	0.07 (0.06, 0.08)	0.07 (0.05, 0.08)
B_I (incubation date)	-0.002 (-0.02, 0.01)	-0.002 (-0.02, 0.01)	-0.002 (-0.02, 0.01)	-0.002 (-0.02, 0.01)

σ_B^2 (between nest variance in intercept)	0.32 (0.29, 0.34)	0.32 (0.30, 0.35)	0.32 (0.30, 0.34)	0.32 (0.29, 0.34)
σ_W^2 (residual variance)	0.29 (0.28, 0.30)	0.25 (0.23, 0.27)	0.28 (0.27, 0.30)	0.29 (0.28, 0.30)
σ_y^2 (annual variance)	5.09 (0.25, 9.78)	4.94 (0.24, 9.73)	5.01 (0.27, 9.79)	5.03 (0.27, 9.75)
$\sigma_{\gamma W}^2$ (between nest variance in slope)	0.64 (0.02, 1.69)	9.47 (7.98, 9.99)	1.97 (0.83, 3.18)	1.75 (0.07, 3.99)
r (intercept/slope)	**-0.67 (-0.79, -0.54)**	-0.04 (-0.16, 0.07)	-0.10 (-0.24, 0.05)	**-0.45 (-0.58, -0.32)**
WAIC	29652.05	29665.14	29663.87	29654.38

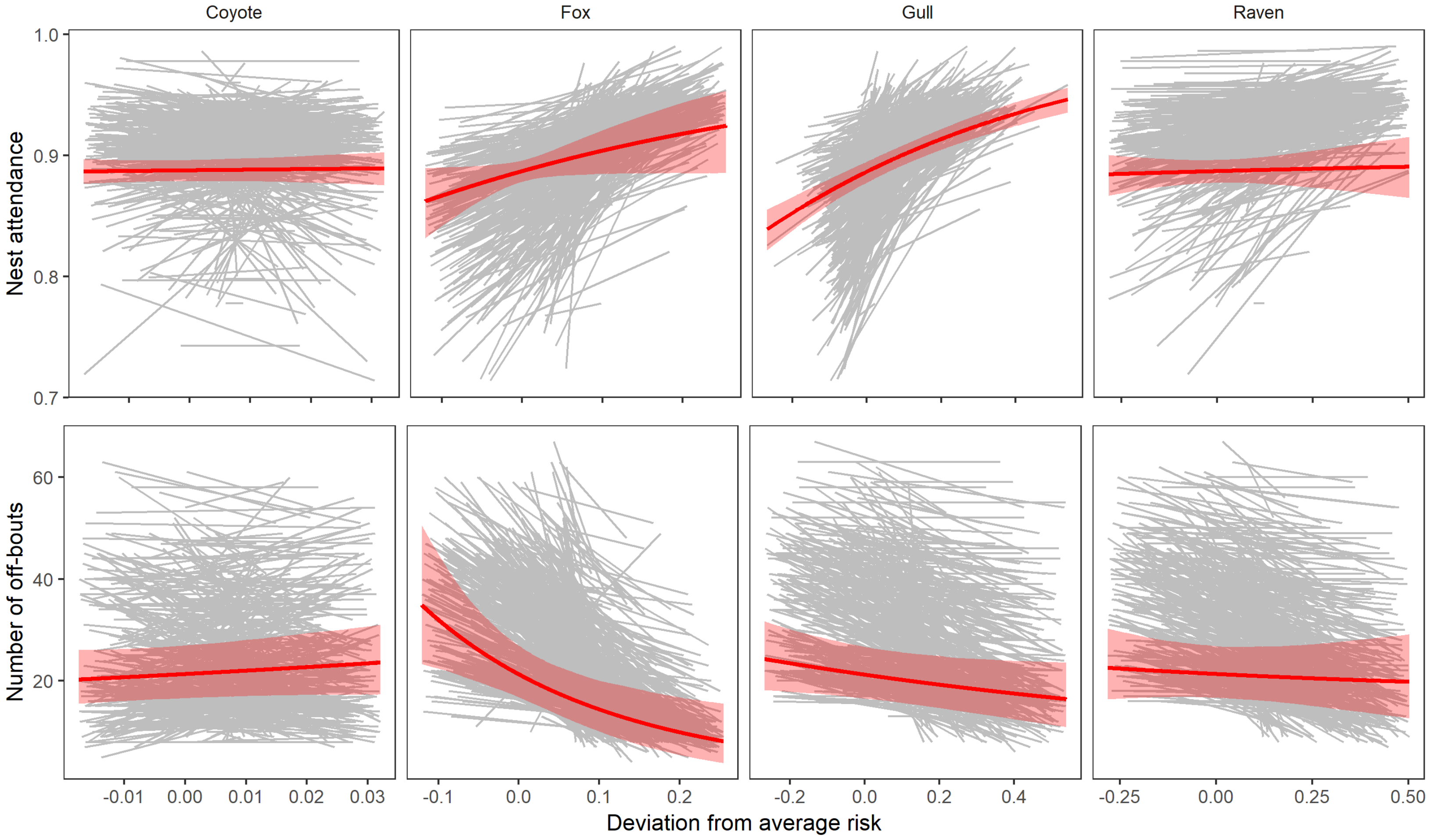

Figure 4-1. Predicted relationships between two measures of incubation behavior and daily deviations from a nest's average risk of predation by specific predators. Red lines indicated the mean within-nest response (B_W) and shaded areas represent 95% Bayesian credible intervals. Grey lines show predicted slopes for individual nests (γ_{Wj}).

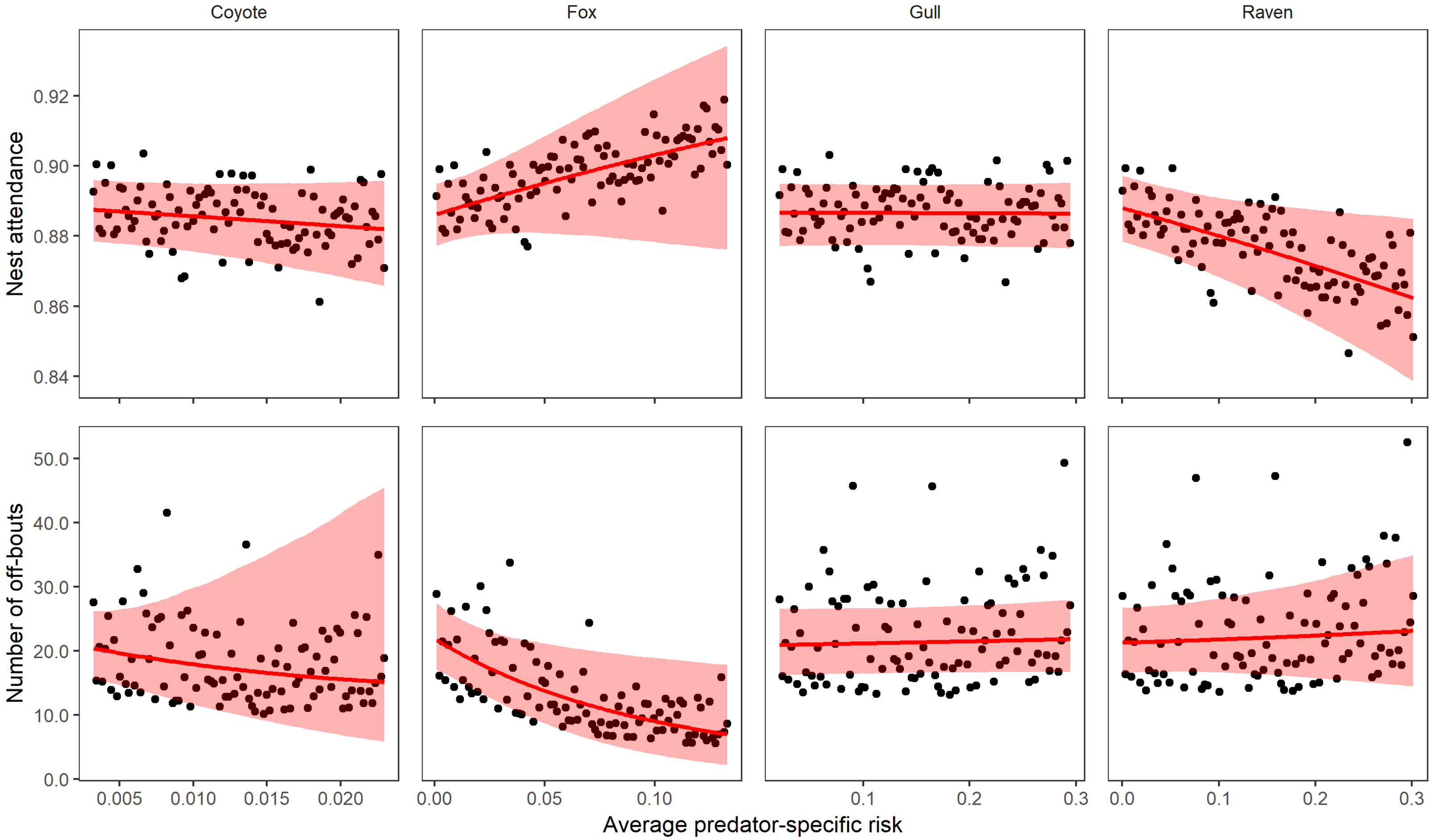

Figure 4-2. Predicted relationships between incubation behaviors (nest attendance and number of off-bouts) and mean predator-specific hazard rates experienced by each nest ($\bar{R}_j$). Red lines indicate the mean between-nest response (B_B) and shaded areas represent 95% Bayesian credible intervals. Points are predicted from individual nest intercepts (γ_{0j}).

LITERATURE CITED

Abrams, P. A., and L. R. Ginzburg (2000). The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology & Evolution 15:337-341.

Ackerman, J. T. (2002). Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. Oikos 99:469-480.

Ackerman, J. T., J. M. Eadie, D. L. Loughman, G. S. Yarris, and M. R. McLandress (2003). The Influence of Partial Clutch Depredation on Duckling Production. The Journal of Wildlife Management 67:576-587.

Ackerman, J. T., S. H. Peterson, D. C. Tsao, and J. Y. Takekawa (2018). California Gull (Larus californicus) Space Use and Timing of Movements in Relation to Landfills and Breeding Colonies. Waterbirds 41:384-401.

Ackerman, J. T., J. Y. Takekawa, C. Strong, N. Athearn, and A. Rex (2006). California Gull distribution, abundance, and predation on waterbird eggs and chicks in south San Francisco Bay. Unpublished final report, US Geological Survey, Western Ecological Research Center, Davis and Vallejo, CA.[Available at: Western Ecological Research Center, US Geological Survey, 3020 State University Dr. East, Modoc Hall, 3rd Floor, Room 3006, Sacramento, CA 95819].

AlRashidi, M., A. Kosztolányi, C. Küpper, I. Cuthill, S. Javed, and T. Székely (2010a). The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover Charadrius alexandrinus. Frontiers in Zoology 7:1-10.

AlRashidi, M., A. Kosztolanyi, C. Kupper, I. C. Cuthill, S. Javed, and T. Szekely (2010b). The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*. Frontiers in Zoology 7:1.

AlRashidi, M., A. Kosztolanyi, M. Shobrak, C. Kupper, and T. Szekely (2011). Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. Animal Behaviour 82:235-243.

Amat, J. A., and J. A. Masero (2004a). How Kentish plovers, *Charadrius alexandrinus*, cope with heat stress during incubation. Behavioral Ecology and Sociobiology 56:26-33.

Amat, J. A., and J. A. Masero (2004b). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Animal Behaviour 67:293-300.

Andes, A. K., T. L. Shaffer, M. H. Sherfy, C. M. Hofer, C. M. Dovichin, and S. N. Ellis-Felege (2019). Accuracy of nest fate classification and predator identification from evidence at nests of Least Terns and Piping Plovers. Ibis 161:286-300.

Andres, B. A., P. A. Smith, R. I. G. Morrison, C. L. Gratto-Trevor, S. C. Brown, and C. A. Friis (2012). Population estimates of North American shorebirds. Wader Study Group Bulletin 119:178-194.

Arditi, R., and L. R. Ginzburg (2012). How species interact: altering the standard view on trophic ecology. Oxford University Press.

Arjo, W. M., E. M. Gese, T. J. Bennett, and A. J. Kozlowski (2007). Changes in kit fox–coyote–prey relationships in the Great Basin Desert, Utah. Western North American Naturalist 67:389-401.

Atwood, T. C., H. P. Weeks, and T. M. Gehring (2004). Spatial ecology of coyotes along a suburban-to-rural gradient. The Journal of Wildlife Management 68:1000-1009.

Baird, P. A. 1976. Comparative ecology of California and ring-billed gulls (*Larus californicus* and *L. delawarensis*). Ph.D., University of Montana.

Ball, J. R., and E. M. Bayne (2012). Using Video Monitoring to Assess the Accuracy of Nest Fate and Nest Productivity Estimates by Field Observation. The Auk 129:438-448.

Barton, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6 https://CRAN.R-project.org/package=MuMIn

Basso, A., and H. Richner (2015). Predator-Specific Effects on Incubation Behaviour and Offspring Growth in Great Tits. PLoS One 10:e0121088.

Batary, P., and A. Baldi (2004). Evidence of an edge effect on avian nest success. Conservation Biology 18:389-400.

Behrens, C., Z. J. Ruff, T. M. Harms, and S. J. Dinsmore (2019). Predator density influences nest attendance of Yellow-headed Blackbirds Xanthocephalus xanthocephalus. Ibis 0.

Belovsky, G. E., D. Stephens, C. Perschon, P. Birdsey, D. Paul, D. Naftz, R. Baskin, C. Larson, C. Mellison, J. Luft, R. Mosley, et al. (2011). The Great Salt Lake Ecosystem (Utah, USA): long term data and a structural equation approach. Ecosphere 2:1-40.

Benson, T. J., J. D. Brown, and J. C. Bednarz (2010). Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225-234.

Berryman, A. A. (1992). The Orgins and Evolution of Predator-Prey Theory. Ecology 73:1530-1535.

Bivand, R. S., E. Pebesma, and V. Gomez-Rubio (2013). Applied spatial data analysis with R, Second edition. Springer, New York.

Boarman, W., M. Patten, R. Camp, and S. Collis (2006). Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. Journal of Arid Environments 67:248-261.

Bolton, M., N. Butcher, F. Sharpe, D. Stevens, and G. Fisher (2007). Remote monitoring of nests using digital camera technology. Journal of Field Ornithology 78:213-220.

Bowman, G. B., and L. Harris (1980). Effect of spatial heterogeneity on ground-nest depredation. The Journal of Wildlife Management:806-813.

Brown, A. L., and J. A. Litvaitis (1995). Habitat features associated with predation of New England cottontails: what scale is appropriate? Canadian Journal of Zoology 73:1005-1011.

Brown, C. R., and M. B. Brown (2001). Avian coloniality. In Current ornithology. Springer 1-82.

Bulla, M., W. Cresswell, A. L. Rutten, M. Valcu, and B. Kempenaers (2015). Biparental incubation-scheduling: no experimental evidence for major energetic constraints. Behavioral Ecology 26:30-37.

Bulla, M., M. Valcu, A. M. Dokter, A. G. Dondua, A. Kosztolányi, A. L. Rutten, B. Helm, B. K. Sandercock, B. Casler, and B. J. Ens (2016). Unexpected diversity in socially synchronized rhythms of shorebirds. Nature.

Bulla, M., M. Valcu, A. L. Rutten, and B. Kempenaers (2014). Biparental incubation patterns in a high-Arctic breeding shorebird: how do pairs divide their duties? Behavioral Ecology 25:152-164.

Burnham, K. P., and D. Anderson (2002). Model Selection and Multi-Model Inference, 2nd ed. Springer.

Burns, F., N. McCulloch, N. Dos Remedios, M. Bolton, and T. Szekely (2013). Sex differences in incubation behaviour but not mortality risk in a threatened shorebird. Ibis 155:877-880.

Burrell, N. S., and M. A. Colwell (2012). Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator. Wildfowl 62:204-223.

Byerly, P. A., R. C. Lonsinger, E. M. Gese, A. J. Kozlowski, and L. P. Waits (2017). Resource partitioning between kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*): a comparison of historical and contemporary dietary overlap. Canadian Journal of Zoology 96:497-504.

Cavitt, J. F., S. L. Jones, N. M. Wilson, J. S. Dieni, T. S. Zimmerman, R. H. Doster, and W. H. Howe (2014). Atlas of breeding colonial waterbirds in the interior western United States.

Chalcraft, D. R., and J. Resetarits, William J (2003). Mapping functional similarity of predators on the basis of trait similarities. The American Naturalist 162:390-402.

Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy (2002). Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306-318.

Chan, K., S. Boutin, T. J. Hossie, C. J. Krebs, M. O'Donoghue, and D. L. Murray (2017). Improving the assessment of predator functional responses by considering alternate prey and predator interactions. Ecology 98:1787-1796.

Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333:1024-1026.

Chiavacci, S. J., T. J. Benson, and M. P. Ward (2018). Linking landscape composition to predator-specific nest predation requires examining multiple landscape scales. Journal of Applied Ecology 55:2082-2092.

Clark, R. G., and T. D. Nudds (1991). Habitat Patch Size and Duck Nesting Success: The Crucial Experiments Have Not Been Performed. Wildlife Society Bulletin (1973-2006) 19:534-543.

Clutton-Brock, T. H. (1991). The evolution of parental care. Princeton University Press, Princeton, N.J.

Colwell, M. A. (2010). Shorebird ecology, conservation, and management. UC Press, Berkeley, California.

Colwell, M. A., J. J. Meyer, M. A. Hardy, S. E. McAllister, A. N. Transou, R. R. Levalley, and S. J. Dinsmore (2011). Western Snowy Plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance crypsis and improve nest survival. Ibis 153:303-311.

Conover, M. R. (1983). Recent changes in Ring-billed and California gull populations in the western United States. The Wilson Bulletin:362-383.

Conover, M. R. (2007). Predator-prey dynamics: the role of olfaction. CRC Press.

Conway, C. J., and T. E. Martin (2000). Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670-685.

Cote, I. M., and W. J. Sutherland (1997). The effectiveness of removing predators to protect bird populations. Conservation Biology 11:395-405.

Creel, S., and J. J. Rotella (2010). Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PLoS One 5:e12918.

Cresswell, W. (2008). Non-lethal effects of predation in birds. Ibis 150:3-17.

Cresswell, W., S. Holt, J. M. Reid, D. P. Whitfield, and R. J. Mellanby (2003). Do energetic demands constrain incubation scheduling in a biparental species? Behavioral Ecology 14:97-102.

Criscuolo, F., G. W. Gabrielsen, J. P. Gendner, and Y. Le Maho (2002). Body mass regulation during incubation in female common eiders *Somateria mollissima*. Journal of Avian Biology 33:83-88.

Crooks, K. R., and M. E. Soule (1999). Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

Cross, P. C., E. J. Maichak, J. D. Rogerson, K. M. Irvine, J. D. Jones, D. M. Heisey, W. H. Edwards, and B. M. Scurlock (2015). Estimating the phenology of elk brucellosis transmission with hierarchical models of cause-specific and baseline hazards. The Journal of Wildlife Management 79:739-748.

Curio, E., G. Klump, and K. Regelmann (1983). An anti-predator response in the great tit (Parus major): is it tuned to predator risk? Oecologia 60:83-88.

Cutler, T. L., and D. E. Swann (1999). Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27.

Cypher, B. L., and K. A. Spencer (1998). Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204-214.

Darrah, A. J., J. B. Cohen, and P. M. Castelli (2017). A Bayesian multinomial logistic exposure model for estimating probabilities of competing sources of nest failure. Ibis 160:23-35.

Dassow, J. A., M. W. Eichholz, J. D. Stafford, and P. J. Weatherhead (2012). Increased nest defence of upland-nesting ducks in response to experimentally reduced risk of nest predation. Journal of Avian Biology 43:61-67.

DeGregorio, B. A., J. H. Sperry, P. J. Weatherhead, S. J. Chiavacci, and T. J. Benson (2016). Nest Predators of North American Birds: Continental Patterns and Implications. BioScience 66:655-665.

Demers, S. A., and C. W. Robinson-Nilsen (2012). Monitoring Western Snowy Plover Nests with Remote Surveillance Systems in San Francisco Bay, California. Journal of Fish and Wildlife Management 3:123-132.

Devineau, O., W. L. Kendall, P. F. Doherty, T. M. Shenk, G. C. White, P. M. Lukacs, and K. P. Burnham (2014). Increased flexibility for modeling telemetry and nest-survival data using the multistate framework. The Journal of Wildlife Management 78:224-230.

Dingemanse, N. J., and N. A. Dochtermann (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. Journal of Animal Ecology 82:39-54.

Dingemanse, N. J., A. J. Kazem, D. Réale, and J. Wright (2010). Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution 25:81-89.

Dinsmore, S. J., and J. J. Dinsmore (2007). Modeling avian nest survival in Program MARK. Studies in Avian Biology 34:73-83.

Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.

Dodds, W. K., K. C. Wilson, R. L. Rehmeier, G. L. Knight, S. Wiggam, J. A. Falke, H. J. Dalgleish, and K. N. Bertrand (2008). Comparing ecosystem goods and services provided by restored and native lands. BioScience 58:837-845.

Dorazio, R. M. (2016). Bayesian data analysis in population ecology: motivations, methods, and benefits. Population Ecology 58:31-44.

Dorset, E. E., S. K. Sakaluk, and C. F. Thompson (2017). Behavioral plasticity in response to perceived predation risk in breeding house wrens. Evolutionary biology 44:227-239.

Douma, J. C., and J. T. Weedon (2019). Analyzing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. Methods in Ecology and Evolution.

Draycott, R. A. H., A. N. Hoodless, M. I. A. Woodburn, and R. B. Sage (2008). Nest predation of Common Pheasants Phasianus colchicus. Ibis 150:37-44.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings of the Royal Society of London B: Biological Sciences 273:701-706.

Ekanayake, K. B., M. A. Weston, D. G. Nimmo, G. S. Maguire, J. A. Endler, and C. Kupper (2015). The bright incubate at night: sexual dichromatism and adaptive incubation division in an open-nesting shorebird. Proceedings of the Royal Society B-Biological Sciences 282:8.

Ellis-Felege, S. N., M. J. Conroy, W. E. Palmer, and J. P. Carroll (2012). Predator reduction results in compensatory shifts in losses of avian ground nests. Journal of Applied Ecology 49:661-669.

Ellis, K. S., J. F. Cavitt, and R. T. Larsen (2015). Factors Influencing Snowy Plover (Charadrius nivosus) Nest Survival at Great Salt Lake, Utah. Waterbirds 38:58-67.

Ellis, K. S., J. F. Cavitt, R. T. Larsen, and D. N. Koons (2018). Using remote cameras to validate estimates of nest fate in shorebirds. Ibis 160:681-687.

Ellis, K. S., R. T. Larsen, R. N. Knight, and J. F. Cavitt (2014). Occupancy and detectability of Snowy Plovers in western Utah: an application to a low density population. Journal of Field Ornithology 85:355-363.

Ergon, T., Ø. Borgan, C. R. Nater, and Y. Vindenes (2018). The utility of mortality hazard rates in population analyses. Methods in Ecology and Evolution 9:2046-2056.

Errington, P. L. (1967). Of Predation and Life, 1st ed. Iowa State University Press, Ames, IA.

Espinheira, P. L., S. L. Ferrari, and F. Cribari-Neto (2008). On beta regression residuals. Journal of Applied Statistics 35:407-419.

Etterson, M. A., B. Olsen, and R. Greenberg (2007). The analysis of covariates in multi-fate Markov chain nest-failure models. Studies in Avian Biology 34:55.

Ferrari, S., and F. Cribari-Neto (2004). Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799-815.

Fischer, J. D., S. H. Cleeton, T. P. Lyons, and J. R. Miller (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. BioScience 62:809-818.

Fontaine, J. J., and T. E. Martin (2006a). Habitat selection responses of parents to offspring predation risk: an experimental test. The American Naturalist 168:811-818.

Fontaine, J. J., and T. E. Martin (2006b). Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428-434.

Forstmeier, W., and I. Weiss (2004). Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Franklin, A. B., D. R. Anderson, R. Gutiérrez, and K. P. Burnham (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Frey, S. N., and M. R. Conover (2006). Habitat use by meso-predators in a corridor environment. Journal of Wildlife Management 70:1111-1118.

Gehring, T. M., and R. K. Swihart (2003). Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109:283-295.

Gelfand, A. E., and A. F. Smith (1990). Sampling-based approaches to calculating marginal densities. Journal of the American statistical Association 85:398-409.

Gelman, A., J. B. Carlin, H. S. Stern, and D. Rubin (2004). Bayesian data analysis 2nd edn Chapman & Hall. CRC, Boca Raton FL.

Ghalambor, C. K., and T. E. Martin (2001). Fecundity-Survival Trade-Offs and Parental Risk-Taking in Birds. Science 292:494-497.

Ghalambor, C. K., and T. E. Martin (2002). Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. Behavioral Ecology 13:101-108.

Ghalambor, C. K., S. I. Peluc, and T. E. Martin (2013). Plasticity of parental care under the risk of predation: how much should parents reduce care? Biology Letters 9.

Gibson, D., E. J. Blomberg, M. T. Atamian, S. P. Espinosa, and J. S. Sedinger (2018). Effects of power lines on habitat use and demography of greater sage-grouse (Centrocercus urophasianus). Wildlife Monographs 200:1-41.

Gochfeld, M. (1984). Antipredator behavior: aggressive and distraction displays of shorebirds. In Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. (Burger, J., and B. Ollas, Burger, J., and B. OllasBurger, J., and B. Ollass), Plenum, New York

Gómez-Serrano, M. Á., and P. López-López (2016). Deceiving predators: linking distraction behavior with nest survival in a ground-nesting bird. Behavioral Ecology:arw157.

Grand, J. B., T. F. Fondell, D. A. Miller, R. M. Anthony, and A. E. Burger (2006). Nest survival in Dusky Canada Geese (*Branta canadensis occidentalis*): use of distrete-time models. The Auk 123:198-210.

Greenhalgh, C. M. (1952). Food Habits of the California Gull in Utah. The Condor 54:302-308.

Griffen, B. D., and J. E. Byers (2006). Intraguild predation reduces redundancy of predator species in multiple predator assemblage. Journal of Animal Ecology 75:959-966.

Grosbois, V., O. Gimenez, J. M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. Møller, and H. Weimerskirch (2008). Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357-399.

Haig, S. M., S. P. Murphy, J. H. Matthews, I. Arismendi, and M. Safeeq (2019). Climate-Altered Wetlands Challenge Waterbird Use and Migratory Connectivity in Arid Landscapes. Scientific Reports 9:4666.

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Princeton University Press.

Heisey, D. M., and B. R. Patterson (2006). A Review of Methods to Estimate Cause-Specific Mortality in Presence of Competing Risks. The Journal of Wildlife Management 70:1544-1555.

Heisey, D. M., T. L. Shaffer, and G. C. White (2007). The ABCs of nest survival: theory and application from a biostatistical perspective. Studies in Avian Biology:13-33.

Henke, S. E., and F. C. Bryant (1999). Effects of Coyote Removal on the Faunal Community in Western Texas. The Journal of Wildlife Management 63:1066-1081.

Hijmans, R. J. (2017). geosphere: Spherical Trigonometry. R package version 1.5-7.

Hijmans, R. J. (2019). raster: Geographic Data Analysis and Modeling. in R package.

Holling, C. S. (1959). The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. The Canadian Entomologist 91:293-320.

Holt, R. D., and J. H. Lawton (1994). The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495-520.

Hossie, T. J., and D. L. Murray (2010). You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. Oecologia 163:395-404.

Hubbs, A. H., and R. Boonstra (1997). Population limitation in Arctic ground squirrels: effects of food and predation. Journal of Animal Ecology:527-541.

Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin (2018). Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. The Condor 120:149-165.

Ibáñez-Álamo, J. D., R. D. Magrath, J. C. Oteyza, A. D. Chalfoun, T. M. Haff, K. A. Schmidt, R. L. Thomson, and T. E. Martin (2015). Nest predation research: recent findings and future perspectives. Journal of Ornithology 156:247-262.

Isaksson, D., J. Wallander, and M. Larsson (2007). Managing predation on ground-nesting birds: The effectiveness of nest exclosures. Biological Conservation 136:136-142.

Ishii, Y., and M. Shimada (2009). The effect of learning and search images on predator–prey interactions. Population Ecology 52:27.

Jackson, H. B., and L. Fahrig (2015). Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52-63.

Jeschke, J. M., M. Kopp, and R. Tollrian (2002). Predator functional responses: Discriminating between handling and digesting prey. Ecological Monographs 72:95-112.

Jeschke, J. M., M. Kopp, and R. Tollrian (2004). Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79:337-349.

Jones, S. L., and G. R. Geupel, Eds. (2007). Beyond Mayfield: Measurements of nest-survival data. Studies in Avian Biology, no. 34.

Juliano, S. (2001). Nonlinear curve fitting: predation and functional response curves. In Design and analysis of ecological experiments (Scheiner, S., and J. Gurevitch, Scheiner, S., and J. GurevitchScheiner, S., and J. Gurevitchs) 178-196.

Katayama, N., T. Amano, and S. Ohori (2010). The Effects of Gravel Bar Construction on Breeding Long-Billed Plovers. Waterbirds 33:162-168.

Kellner, K. (2018). jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses.

Kentie, R., J. C. Hooijmeijer, K. B. Trimbos, N. M. Groen, and T. Piersma (2013). Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. Journal of Applied Ecology 50:243-251.

Kluever, B. M., and E. M. Gese (2017). Evaluating the influence of water developments on the demography and spatial ecology of a rare, desert-adapted carnivore: the kit fox (Vulpes macrotis). Journal of Mammalogy 98:815-826.

Koons, D. N., L. M. Aubry, and R. F. Rockwell (2019). Liberalized harvest regulations have not affected overabundant Snow Geese in Northern Manitoba. The Condor: Ornithological Applications.

Kozlowski, A. J., E. M. Gese, and W. M. Arjo (2008). Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. The American Midland Naturalist 160:191-208.

Kristan III, W. B., and W. I. Boarman (2007). Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. Ecological Applications 17:1703-1713.

Kulmatiski, A., K. H. Beard, L. A. Meyerson, J. R. Gibson, and K. E. Mock (2010). Nonnative *Phragmites australis* invasion into Utah wetlands. Western North American Naturalist 70:541-552.

Laake, J. L., and E. A. Rexstad (2012). RMark – An Alternative Approach to Building Linear Models in MARK. In Program MARK: 'A Gentle Introduction' (Cooch, E., and G. C. White, Cooch, E., and G. C. WhiteCooch, E., and G. C. Whites). http://www.phidot.org/software/mark/docs/book C-1 - C-115.

Lahti, D. C. (2001). The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365-374.

Laidlaw, R. A., J. Smart, M. A. Smart, and J. A. Gill (2015). The influence of landscape features on nest predation rates of grassland-breeding waders. Ibis 157:700-712.

Lariviere, S. (1999). Reasons why predators cannot be inferred from nest remains. Condor 101:718-721.

Levin, S. A. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73:1943-1967.

Liebezeit, J. R., and S. Zack (2008). Point Counts Underestimate the Importance of Arctic Foxes as Avian Nest Predators: Evidence from Remote Video Cameras in Arctic Alaskan Oil Fields. Arctic 61:153-161.

Liermann, M., and R. Hilborn (2001). Depensation: evidence, models and implications. Fish and Fisheries 2:33-58.

Lima, S. L. (2009). Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart (2005). Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications 15:1504-1514.

Long, A. L., K. M. Kettenring, C. P. Hawkins, and C. M. U. Neale (2017). Distribution and Drivers of a Widespread, Invasive Wetland Grass, Phragmites australis, in Wetlands of the Great Salt Lake, Utah, USA. Wetlands 37:45-57.

Lonsinger, R. C., E. M. Gese, L. L. Bailey, and L. P. Waits (2017). The roles of habitat and intraguild predation by coyotes on the spatial dynamics of kit foxes. Ecosphere 8.

Lor, S., and R. A. Malecki (2006). Breeding Ecology and Nesting Habitat Associations of Five Marsh Bird Species in Western New York. Waterbirds 29:427-436.

Lowry, J. H. J., R. D. Ramsey, K. Boykin, D. Bradford, P. Comer, S. Falzarano, W. Kepner, J. Kirby, L. Langs, J. Prior-Magee, G. Manis, et al. (2005). Southwest Regional Gap Analysis Project: Final Report on Land Cover Mapping Methods. RS/GIS Laboratory, Utah State University, Logan, USA.

Lyons, T. P., J. R. Miller, D. M. Debinski, and D. M. Engle (2015). Predator identity influences the effect of habitat management on nest predation. Ecological Applications 25:1596-1605.

Ma, Z., Y. Cai, B. Li, and J. Chen (2010). Managing Wetland Habitats for Waterbirds: An International Perspective. Wetlands 30:15-27.

Mabee, T. J. (1997). Using eggshell evidence to determine nest fate of shorebirds. Wilson Bulletin 109:307-313.

Mabee, T. J., and V. B. Estelle (2000). Nest fate and vegetation characteristics for Snowy Plover and Killdeer in Colorado, USA. Wader Study Group Bulletin 93:67-72.

Mabee, T. J., A. M. Wildman, and C. B. Johnson (2006). Using egg flotation and eggshell evidence to determine age and fate of Arctic shorebird nests. Journal of Field Ornithology 77:163-172.

Madden, C. F., B. Arroyo, and A. Amar (2015). A review of the impacts of corvids on bird productivity and abundance. Ibis 157:1-16.

Malzer, I., and B. Helm (2015). The Seasonal Dynamics of Artificial Nest Predation Rates along Edges in a Mosaic Managed Reedbed. PLoS One 10:e0140247.

Martin, T. E. (1993). Nest predation and nest sites: new perspectives on old patterns. BioScience 43:523-532.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

Martin, T. E., and C. K. Ghalambor (1999). Males feeding females during incubation: Required by microclimate or constrained by nest predation? The American Naturalist 153:131-139.

Martin, T. E., P. Martin, C. Olson, B. Heidinger, and J. Fontaine (2000a). Parental care and clutch sizes in North and South American birds. Science 287:1482-1485.

Martin, T. E., J. Scott, and C. Menge (2000b). Nest predation increases with parental activity; separating nest site and parental activity effect. Proceedings of the Royal Society B 267:2287-2293.

Massaro, M., A. Starling-Windhof, J. V. Briskie, and T. E. Martin (2008). Introduced Mammalian Predators Induce Behavioural Changes in Parental Care in an Endemic New Zealand Bird. PLoS One 3:e2331.

Mayfield, H. F. (1961). Nesting success calculated from exposure. The Wilson Bulletin 73:255-261.

McCoy, M. W., A. C. Stier, and C. W. Osenberg (2012). Emergent effects of multiple predators on prey survival: the importance of depletion and the functional response. Ecology Letters 15:1449-1456.

McKinnon, L., D. Berteaux, and J. Bêty (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. The Auk 131:619-628.

McKinnon, L., and J. Bêty (2009). Effect of camera monitoring on survival rates of High-Arctic shorebird nests. Journal of Field Ornithology 80:280-288.

Melles, S., D. Badzinski, M.-J. Fortin, F. Csillag, and K. Lindsay (2009). Disentangling habitat and social drivers of nesting patterns in songbirds. Landscape Ecology 24:519.

Mezquida, E. T., S. J. Slater, and C. W. Benkman (2006). Sage-Grouse and indirect interactions: Potential implications of coyote control on Sage-Grouse populations. The Condor 108:747-759.

Miller, D. A., J. B. Grand, T. F. Fondell, and M. Anthony (2006). Predator functional response and prey survival: direct and indirect interactions affecting a marked prey population. Journal of Animal Ecology 75:101-110.

Morris, D. W. (1987). Ecological scale and habitat use. Ecology 68:362-369.

Murdoch, W. W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335-354.

Murphy, E., and P. Bradfield (1992). Change in diet of stoats following poisoning of rats in a New Zealand forest. New Zealand journal of ecology:137-140.

Murray, N. J., P. P. Marra, R. A. Fuller, R. S. Clemens, K. Dhanjal-Adams, K. B. Gosbell, C. J. Hassell, T. Iwamura, D. Melville, and C. D. Minton (2018). The large-scale drivers of population declines in a long-distance migratory shorebird. Ecography 41:867-876.

Nelson, E. H., C. E. Matthews, and J. A. Rosenheim (2004). Predators reduce prey population growth by inducing changes in prey behavior. Ecology 85:1853-1858.

Nelson, J. B., and P. H. Baird (2001). Seabird communication and displays. CRC Press, Boca Raton, FL.

Nelson, J. L., B. L. Cypher, C. D. Bjurlin, and S. Creel (2007). Effects of Habitat on Competition Between Kit Foxes and Coyotes. The Journal of Wildlife Management 71:1467-1475.

Newsome, S. D., H. M. Garbe, E. C. Wilson, and S. D. Gehrt (2015). Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115-128.

Newton, I. (1998). Population limitation in birds. Academic press.

Norris, K. (2004). Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology 41:413-426.

Northrup, J. M., and B. D. Gerber (2018). A comment on priors for Bayesian occupancy models. PLoS One 13:e0192819.

Norton, D. W. (1972). Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164-176.

O'Neil, S. T., P. S. Coates, B. E. Brussee, P. J. Jackson, K. B. Howe, A. M. Moser, L. J. Foster, and D. J. Delehanty (2018). Broad-scale occurrence of a subsidized avian predator: Reducing impacts of ravens on sage-grouse and other sensitive pr. Journal of Applied Ecology 55:2641-2652.

Page, G. W., L. E. Stenzel, and C. A. Ribic (1985). Nest site selection and clutch predation in the Snowy Plover. Auk 102:347-353.

Page, G. W., L. E. Stenzel, J. S. Warriner, J. C. Warriner, and P. W. Paton (2009). Snowy Plover (*Charadrius nivosus*). The Birds of North America Online (A. Poole, Ed.).

Page, G. W., L. E. Stenzel, D. W. Winkler, and C. W. Swarth (1983). Spacing out at Mono Lake: breeding success, nest density, and predation in the Snowy Plover. The Auk 100:13-24.

Paton, P. W. C. (1994). Survival Estimates for Snowy Plover Breeding at Great Salt Lake, Utah. The Condor 96:1106-1109.

Paton, P. W. C. (1995). Breeding biology of Snowy Plovers at Great Salt Lake, Utah. The Wilson Bulletin 107:275-288.

Patrick, A. M., and M. A. Colwell (2018). Annual variation in distance to nearest neighbor nest decreases with population size in snowy plovers. Wader Study Group Bull 124.

Pebesma, E. J., and R. S. Bivand (2005). Classes and methods for spatial data in R

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor (2008). Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830-835.

Peterson, S. A., and M. A. Colwell (2014). Experimental evidence that scare tactics and effigies reduce corvid occurrence. Northwestern Naturalist 95:103-112.

Phillips, M. L., W. R. Clark, M. A. Sovada, D. J. Horn, R. R. Koford, and R. J. Greenwood (2003). Predator selection of prairie landscape features and its relation to duck nest success. Journal of Wildlife Management 67:104-114.

Pietz, P. J., and D. A. Granfors (2000). Identifying predators and fates of grassland passerine nests using miniature video cameras. The Journal of Wildlife Management:71-87.

Plummer, M. (2017). JAGS version 4.3.0 user manual.

Polis, G. A., C. A. Myers, and R. D. Holt (1989). The Ecology and Evolution of Intraguild Predation: Potential Competitors That Eat Each Other. Annual Review of Ecology and Systematics 20:297-330.

Preisser, E. L., D. I. Bolnick, and M. F. Benard (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501-509.

Pretelli, M. G., J. P. Isacch, and D. A. Cardoni (2016). Variation in parental care in the spectacled tyrant Hymenops perspicillatus is associated with increased nest predation in grassland fragments. Journal of Ornithology 157:451-460.

Quakenbush, L., R. Suydam, T. Obritschkewitsch, and M. Deering (2004). Breeding biology of Steller's eiders (Polysticta stelleri) near Barrow, Alaska, 1991-99. Arctic:166-182.

R Development Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.

Ralls, K., and P. J. White (1995). Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76:723-729.

Rannap, R., T. Kaart, H. Pehlak, S. Kana, E. Soomets, and K. Lanno (2017). Coastal meadow management for threatened waders has a strong supporting impact on meadow plants and amphibians. Journal for Nature Conservation 35:77-91.

Richardson, T., T. Gardali, and S. H. Jenkins (2009). Review and meta-analysis of camera effects on avian nest success. The Journal of Wildlife Management 73:287-293.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Rioux, S., D. L. Amirault-Langlais, and F. Shaffer (2011). Piping Plovers make decisions regarding dispersal based on personal and public information in a variable coastal ecosystem. Journal of Field Ornithology 82:32-43.

Robel, R., J. Briggs, A. Dayton, and L. Hulbert (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management:295-297.

Roberts, A. J. (2013). Avian diets in a saline ecosystem: Great Salt Lake, Utah, USA. Human-Wildlife Interactions 7:158-168.

Roper, J. J., and R. R. Goldstein (1997). A test of the Skutch hypothesis: does activity at nests increase nest predation risk? Journal of Avian Biology:111-116.

Rotella, J., E. Cooch, and G. White (2009). Nest survival models. Cooch E White G (eds) Chapter 17.

Royle, N. J., A. F. Russell, and A. J. Wilson (2014). The evolution of flexible parenting. Science 345:776-781.

Saalfeld, S. T., W. C. Conway, D. A. Haukos, and W. P. Johnson (2012). Snowy plover nest site selection, spatial patterning, and temperatures in the Southern High Plains of Texas. The Journal of Wildlife Management 76:1703-1711.

Saalfeld, S. T., B. L. Hill, and R. B. Lanctot (2013). Shorebird responses to construction and operation of a landfill on the Arctic Coastal Plain. Condor 115:816-829.

Sala, O. E., F. Stuart Chapin , III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, et al. (2000). Global Biodiversity Scenarios for the Year 2100. Science 287:1770-1774.

Sandercock, B. K., E. B. Nilsen, H. Broseth, and H. C. Pedersen (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology 80:244-258.

Schaub, M., and J.-D. Lebreton (2004). Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. Animal Biodiversity and Conservation 27:73-85.

Schmidt, K. A. (1999). Foraging Theory as a Conceptual Framework for Studying Nest Predation. Oikos 85:151-160.

Schmidt, K. A., and C. J. Whelan (1998). Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. The American Naturalist 152:393-402.

Schmitz, O. J. (2007). Predator diversity and trophic interactions. Ecology 88:2415-2426.

Schmitz, O. J., J. R. B. Miller, A. M. Trainor, and B. Abrahms (2017). Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. Ecology 98:2281-2292.

Scopel, L. C., and A. W. Diamond (2017). The case for lethal control of gulls on seabird colonies. Journal of Wildlife Management 81:572-580.

Scopel, L. C., and A. W. Diamond (2018). Predation and food-weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (Sterna paradisaea). Canadian Journal of Zoology 96:13-22.

Seber, G. A. (1986). A review of estimating animal abundance. Biometrics:267-292.

Senner, N. R., J. N. Moore, S. T. Seager, S. Dougill, K. Kreuz, and S. E. Senner (2018). A salt lake under stress: Relationships among birds, water levels, and invertebrates at a Great Basin saline lake. Biological Conservation 220:320-329.

Servanty, S., R. Choquet, É. Baubet, S. Brandt, J.-M. Gaillard, M. Schaub, C. Toïgo, J.-D. Lebreton, M. Buoro, and O. Gimenez (2010). Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach. Ecology 91:1916-1923.

Sheriff, M. J., and J. S. Thaler (2014). Ecophysiological effects of predation risk; an integration across disciplines. Oecologia 176:607-611.

Sih, A., G. Englund, and D. Wooster (1998). Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350-355.

Sih, A., Philip Crowley, M. McPeek, J. Petranka, and K. Strohmeier (1985). Predation, Competition, and Prey Communities: A Review of Field Experiments. Annual Review of Ecology and Systematics 16:269-311.

Smart, J., J. A. Gill, W. J. Sutherland, and A. R. Watkinson (2006). Grassland-breeding waders: identifying key habitat requirements for management. Journal of Applied Ecology 43:454-463.

Smith, P. A., and D. B. Edwards (2018). Deceptive nest defence in ground-nesting birds and the risk of intermediate strategies. PLoS One 13:e0205236.

Smith, P. A., H. G. Gilchrist, and J. N. M. Smith (2007). Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109:15-31.

Smith, P. A., I. Tulp, H. Schekkerman, H. G. Gilchrist, and M. R. Forbes (2012). Shorebird incubation behaviour and its influence on the risk of nest predation. Animal Behaviour 84:835-842.

Solomon, M. (1949). The natural control of animal populations. The Journal of Animal Ecology:1-35.

Spaans, B., H. Blijleven, I. Popov, M. Rykhlikova, and B. Ebbinge (1998). Dark-bellied Brent Geese Branta bernicla bernicla forego breeding when Arctic Foxes Alopex lagopus are present during nest initiation. Ardea 86:11-20.

Spautz, H., N. Nur, D. Stralberg, and Y. Chan (2006). Multiple-scale habitat relationships of tidal-marsh breeding birds in the San Francisco Bay estuary. Studies in Avian Biology 32:247.

Stamps, J. A. (1988). Conspecific attraction and aggregation in territorial species. The American Naturalist 131:329-347.

Stearns, S. C. (1992). The evolution of life histories.

Stelbrink, P., A. Grendelmeier, D. Schabo, R. Arlettaz, F. Hillig, and G. Pasinelli (2019). Does acoustically simulated predation risk affect settlement and reproduction of a migratory passerine? Ethology.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey (2004). Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101-110.

Stephens, S. E., J. J. Rotella, M. S. Lindberg, M. L. Taper, and J. K. Ringelman (2005). Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecological Applications 15:2137-2149.

Stiehl, R. B., and S. N. Trautwein (1991). Variations in diets of nesting Common Ravens. The Wilson Bulletin:83-92.

Stolley, D. S., J. A. Bissonette, and J. A. Kadlec (1999). Limitations on Canada Goose production at Fish Springs National Wildlife Refuge. Great Basin Naturalist 59:245-252.

Stuber, E. F., L. F. Gruber, and J. J. Fontaine (2017). A Bayesian method for assessing multi-scale species-habitat relationships. Landscape Ecology 32:2365-2381.

Studds, C. E., B. E. Kendall, N. J. Murray, H. B. Wilson, D. I. Rogers, R. S. Clemens, K. Gosbell, C. J. Hassell, R. Jessop, and D. S. Melville (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature communications 8:14895.

Suvorov, P., J. Svobodová, and T. Albrecht (2014). Habitat edges affect patterns of artificial nest predation along a wetland-meadow boundary. Acta Oecologica 59:91-96.

Swaisgood, R. R., L. A. Nordstrom, J. G. Schuetz, J. T. Boylan, J. J. Fournier, and B. Shemai (2018). A management experiment evaluating nest-site selection by beach-nesting birds. The Journal of Wildlife Management 82:192-201.

Swift, R. J., A. D. Rodewald, and N. R. Senner (2018). Context-dependent costs and benefits of a heterospecific nesting association. Behavioral Ecology 29:974-983.

Székely, T. (2019). Why study plovers? The significance of non-model organisms in avian ecology, behaviour and evolution. Journal of Ornithology:1-11.

Templeton, C. N., E. Greene, and K. Davis (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308:1934-1937.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin (2006). Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759-768.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin (1998). Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.

Thomas, S. M., J. E. Lyons, B. A. Andres, E. Elliot-Smith, E. Palacios, J. F. Cavitt, J. A. Royle, S. D. Fellows, K. Maty, W. H. Howe, E. Mellink, et al. (2012). Population size of Snowy Plovers breeding in North America. Waterbirds 35:1-14.

Thornton, D. H., and R. J. Fletcher (2014). Body size and spatial scales in avian response to landscapes: a meta-analysis. Ecography 37:454-463.

Tinbergen, J., and J. Williams (2002). Energetics of incubation. In Avian incubation: behaviour, environment and evolution (DC, D., DC, D.)DC, D.s). Oxford University Press, Oxford 299–313.

Tozer, D. C., E. Nol, and K. F. Abraham (2010). Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. Wetlands Ecology and Management 18:679-693.

Trexler, J. C., C. E. McCulloch, and J. Travis (1988). How can the functional reponse best be determined? Oecologia 76:206-214.

Tulp, I., and H. Schekkerman (2006). Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. Journal of Avian Biology 37:207-218.

USFWS (2007). Recovery Plan for the Pacific Coast Population of the Western Snowy Plover (*Charadrius alexandrinus nivosus*). Endangered Species Program. Sacramento, California.

USFWS (2012). Endangered and Threatened Wildlife and Plants; Revised Designation of Critical Habitat for the Pacific Coast Population of the Western Snowy Plover.

van de Pol, M., and J. Wright (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. Animal Behaviour 77:753.

van Kleef, H., F. Willems, A. E. Volkov, J. J. H. R. Smeets, D. Nowak, and A. Nowak (2007). Dark-bellied brent geese Branta b. bernicla breeding near snowy owl Nyctea scandiaca nests lay more and larger eggs. Journal of Avian Biology 38:1-6.

Vance-Chalcraft, H. D., and D. A. Soluk (2005). Estimating the Prevalence and Strength of Non-Independent Predator Effects. Oecologia 146:452-460.

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman 2018. https://CRAN.R-project.org/package=loo.

Vincze, O., A. Kosztolányi, Z. Barta, C. Küpper, M. Alrashidi, J. A. Amat, A. Argüelles Ticó, F. Burns, J. Cavitt, and W. C. Conway (2016). Parental cooperation in a changing climate: fluctuating environments predict shifts in care division. Global Ecology and Biogeography.

Vincze, O., T. Székely, C. Küpper, M. AlRashidi, J. A. Amat, A. A. Ticó, D. Burgas, T. Burke, J. Cavitt, J. Figuerola, M. Shobrak, et al. (2013). Local Environment but Not Genetic Differentiation Influences Biparental Care in Ten Plover Populations. PLoS One 8:e60998.

Walters, C. J. (1986). Adaptive management of renewable resources. Macmillan Publishers Ltd.

Wasserman, R. J., M. E. Alexander, T. Dalu, B. R. Ellender, H. Kaiser, and O. L. F. Weyl (2016). Using functional responses to quantify interaction effects among predators. Functional Ecology 30:1988-1998.

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. Journal of Machine Learning Research 11:3571-3594.

Webb, D. (1987). Thermal tolerance of avian embryos: a review. The Condor 89:874-898.

Webb, W. C., W. I. Boarman, and J. T. Rotenberry (2009). Movements of Juvenile Common Ravens in an Arid Landscape. The Journal of Wildlife Management 73:72-81.

Weiser, E. L., and A. N. Powell (2011). Reduction of Garbage in the Diet of Nonbreeding Glaucous Gulls Corresponding to a Change in Waste Management. Arctic 64:220-226.

Westneat, D. F., M. I. Hatch, D. P. Wetzel, and A. L. Ensminger (2011). Individual variation in parental care reaction norms: integration of personality and plasticity. The American Naturalist 178:652-667.

Wiens, J. A. (1989). Spatial scaling in ecology. Functional Ecology 3:385-397.

Williams, G. E., and P. B. Wood (2002). Are Traditional Methods of Determining Nest Predators and Nest Fates Reliable? An Experiment with Wood Thrushes (*Hylocichla mustelina*) Using Miniature Video Cameras. The Auk 119:1126-1132.

Wurtsbaugh, W. A., C. Miller, S. E. Null, R. J. DeRose, P. Wilcock, M. Hahnenberger, F. Howe, and J. Moore (2017). Decline of the world's saline lakes. Nature Geoscience 10:816.

Yerkes, T. (1998). The influence of female age, body mass, and ambient conditions on redhead incubation constancy. The Condor 100:62-68.

Yoon, J., B.-S. Kim, E.-J. Joo, and S.-R. Park (2016). Nest predation risk influences a cavity-nesting passerine during the post-hatching care period. Scientific Reports 6:31989.

Zanette, L. Y., M. Clinchy, and J. P. Suraci (2014). Diagnosing predation risk effects on demography: can measuring physiology provide the means? Oecologia 176:637-651.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy (2011). Perceived Predation Risk Reduces the Number of Offspring Songbirds Produce per Year. Science 334:1398-1401.

Zedler, J. B., and S. Kercher (2004). Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.

Zuur, A. F., E. N. Ieno, and C. S. Elphick (2010). A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

APPENDIX – CHAPTER 2

Table S1. Total number of nests used to evaluate hazard rates of predator-specific nest mortality for snowy plovers (*Charadrius nivosus*) at two study areas in Utah, USA between 2011 and 2017.

Year	Great Salt Lake	Western Utah	Total
2011		7	7
2012		12	12
2013	2	7	9
2014	50	42	92
2015	44	26	70
2016	53	101	154
2017	45	84	129
Total	194	279	473

Table S2. Posterior estimates of time-averaged nest mortality hazard rates (h_j) for each predator, based on the reference model (Eqn. 2).

Mean estimate	2.50%	97.50%	Predator
Great Salt Lake			
0.0054	0.0007	0.0128	Fox
0.0039	0.0002	0.0099	Coyote
0.0231	0.0074	0.0445	Raven
0.0101	0.0012	0.0175	Gull
Western Utah			
0.006	0.0021	0.0117	Fox
0.0018	0.0001	0.0053	Coyote
0.0017	0.00002	0.0061	Raven

Table S3. Posterior beta estimates from the functional response model which estimated nest mortality hazard rates (h_j) for each predator as a function of snowy plover nest abundance.

Predator	Parameter	Mean estimate	2.50%	97.50%
Fox	Linear	2.095	0.765	3.428
	Quadratic	-0.651	-0.938	-0.351
	Cubic	0.005	-0.377	0.386
Coyote	Linear	-0.008	-0.203	0.186
	Quadratic	-0.086	-1.276	1.145
	Cubic	0.002	-0.993	0.990
Raven	Linear	1.467	0.124	2.809
	Quadratic	-1.528	-2.657	-0.433
	Cubic	0.006	-0.425	0.436
Gull	Linear	-1.890	-3.288	-0.545
	Quadratic	-0.099	-0.606	0.402
	Cubic	0.012	-1.328	1.323

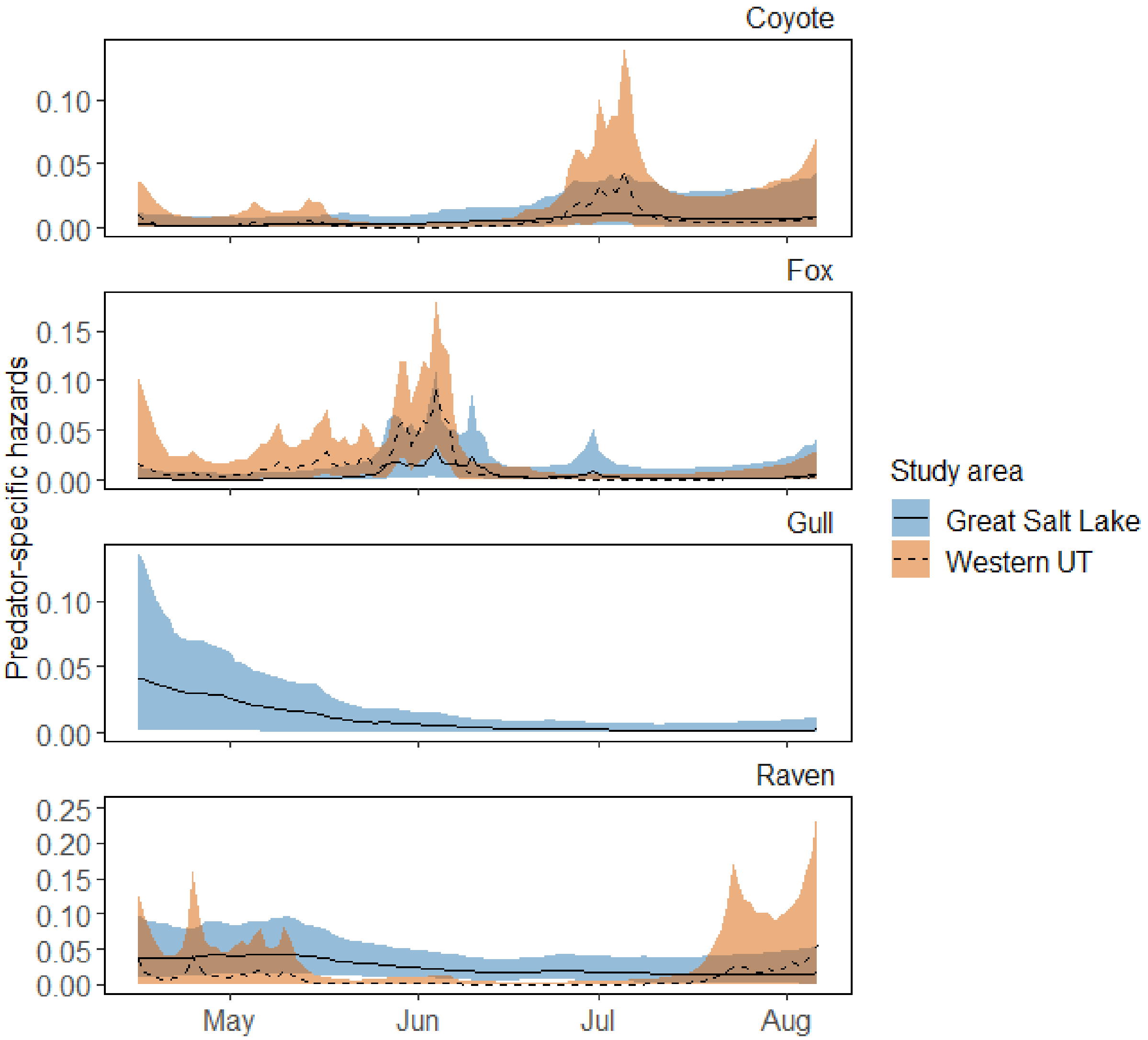

Figure S1. Posterior estimates of predator-specific mortality hazard rates for snowy plover nests across the breeding season from the AR model. Lines indicate the mean estimate and shaded areas represent 95% Bayesian credible intervals. Note that the y-axes are not consistent among panels to allow for visualization of predator-specific patterns.

Chapter 2 MCMC Iterations

Reference model

Number of iterations = 20000
Number of burn-in =5000
Number of adapt = 5000
Number thinned = 5
Number of chains = 3
Number of samples retained = 9000

Autoregressive smoothing and functional response models
Number of iterations = 200000
Number of burn-in = 50000
Number of adapt = 50000
Number thinned = 50
Number of chains = 3
Number of samples retained = 9000