Nest Predators of North American Birds: Continental Patterns and Implications

BRETT A. DEGREGORIO, SCOTT J. CHIAVACCI, THOMAS J. BENSON, JINELLE H. SPERRY, AND PATRICK J. WEATHERHEAD

Identifying nest predators is of fundamental importance to understanding avian breeding ecology and can contribute to identifying broadscale nest-predation patterns. We reviewed 53 North American nest-predator studies, comprising more than 4000 camera-monitored nests, to explore geographic patterns in predator identity and how predation varied with predator richness, habitat, nest height, and bird size. Overall, mesopredators (at high latitudes) and snakes (at low latitudes) were the most frequent nest-predator guilds. Predation by rodents was greatest in the Great Plains and boreal forest and by corvids in the Southwest. Predation by different guilds was often correlated. Predator richness was greatest at midlatitudes but was a poor predictor of predation probability. Nest height and habitat influenced predator-specific predation. The richness of predator species was not influenced by bird body size, nesting height, or habitat type. Our results enable the prediction of regionally influential predators, highlight knowledge gaps, and provide a foundation for further exploration.

Keywords: avian ecology, breeding behavior, nest cameras, predator–prey interactions, predator identity

Documenting the causes and consequences of variation in reproductive success is central to many questions in ecology and evolution. This is particularly true in ornithology, in which understanding what influences reproductive success has been a research focus for decades. Nest predation is the primary cause of nest failure for most birds (Ricklefs 1969, Martin 1993) and is often the most important contributor to variation in reproductive success. Therefore, nest predation has played a fundamental role in the evolution of avian life histories (Martin 1988, 1993, Latif et al. 2012). Despite the extensive documentation of the extent and consequences of nest predation for birds, however, a more complete understanding of nest predation has been limited by our lack of reliable information on the identity of the predators (Liebezeit and George 2002, Weatherhead and Blouin-Demers 2004, Benson et al. 2010). Knowing which predators are responsible for nest failure is essential for understanding the potential for birds to reduce their risk of predation, given that responses to predation depend on the diversity and types of predators involved. Furthermore, because nest predation can also limit the viability of bird populations (Robinson and Wilcove 1994), conservation efforts to reduce predation are likely to benefit from knowing which predator species to target. The difficulty in observing avian nest predators stands in contrast to the ease of observing nests and adults that has made birds such attractive research subjects. This shortcoming is being overcome with the increasing use of miniaturized video cameras for identifying nest predators (Thompson et al. 1999, Cox et al. 2012a). Here, we review the data accumulated from nest-camera studies to identify broad geographical and ecological patterns in nest-predator identity.

Nest-camera studies have revealed both that communities of nest predators are more diverse (e.g., Weidinger 2008) and that the dominant predators are different from what was once thought (Peterson et al. 2004, Liebezeit and Zack 2008). For example, nest predators may vary on small spatial scales based on habitat differences (Thompson and Burhans 2003) and the nest-site characteristics of bird species (Cox et al. 2012b). Furthermore, identifying nest predators has allowed researchers to focus on important predator guilds (Weatherhead and Blouin-Demers 2004, Thompson and Ribic 2012, DeGregorio et al. 2014a) and to elucidate habitat, temporal, and climatic factors that predict the vulnerability of nests to particular predators (e.g., Sperry et al. 2008, 2009, Benson et al. 2010, Klug et al. 2010, Weatherhead et al. 2010, Cox et al. 2012b, 2012c, Reidy and Thompson 2012, Cox et al. 2013). Two recent analyses illustrated the value in examining broadscale patterns in nest predation due to different predators. First, using five

camera studies from the Midwest and the southern United States, Thompson and Ribic (2012) found that predation by several dominant predators (e.g., snakes; mammals; and fire ants, *Solenopsis invicta*) varied by latitude and habitat. In the second, DeGregorio and colleagues (2014a) used data from 53 camera studies to show how nest predation by different snake species varied across North America and identified ecological factors associated with nest predation by snakes.

Our goal here was to expand on those previous studies by combining data from 53 North American nest-camera studies and using data for all nest predators identified to determine how nest-predator communities vary at a continental scale on the basis of geography and biological and habitat-related factors. Specifically, we explore how a nest's geographic location affects the probability it will be preyed on by different types of predators. We also examine how nesting habitat, nest height, and the body size of nesting birds influence vulnerability to different predators. For example, ground-nesting species may be vulnerable to predation by mesopredators, whereas canopy nesters may be more vulnerable to avian predators (Söderström et al. 1998, Reidy and Thompson 2012). Evidence also indicates that even at the same locations, different nest-site characteristics influence the vulnerability of nests to different predators. Cox and colleagues (2012b) showed that shrub-nesting indigo buntings (*Passerina cyanea*) experienced high predation rates from avian predators, mesopredators, and snakes relative to intermediate-height nesting Acadian flycatchers (*Empidonax virescens*). Conversely, the predators of shrub-nesting Swainson's warblers (*Limnothlypis swainsonii*) and canopy-nesting Mississippi kites (*Ictinia mississippiensis*) were largely the same at a study site in Arkansas despite profound differences in the nesting height and body size of these two bird species (Bader and Bednarz 2009, Benson et al. 2010, Chiavacci et al. 2014). The size of the nesting bird may also influence predator identity and richness, given that some birds may vigorously defend their nests and the effectiveness of nest defense may depend on the size of birds (Montgomerie and Weatherhead 1988, Pietz and Granfors 2005), as well as the fact that some predators such as snakes are gape limited, thereby reducing the vulnerability of some nests to snake predation. Finally, geographic and nesting-habitat patterns in predation may also be a function of the habitat preferences of predator species, which influences their distribution and therefore their role as nest predators across a landscape (Dijak and Thompson 2000, Blouin-Demers and Weatherhead 2001, Chalfoun et al. 2002, DeGregorio et al. 2014b).

We test several hypotheses regarding the ecological consequences resulting from variation in predator assemblages. First, the incidence of nest predation should vary with the richness of nest predators (or predator foraging strategies) at a location. A positive association between predation and predator richness could occur because it is more difficult for birds to nest or behave in ways that reduce the risk from one type of predator without increasing the risk from another (Filliater et al. 1994, Liebezeit and George 2002). Alternatively, when there are fewer types of predators (e.g., Liebezeit and Zack 2008), those predators may be able to specialize and become more effective, thereby increasing the overall risk of nest predation. Predator richness might also interact with nest characteristics to affect predation risk. We test the prediction that shrubland nests should experience predation from a richer suite of predators because this habitat is transitional between forest and grassland and should be exposed to predators from both habitats. Similarly, nests at intermediate heights should also have the most diverse group of nest predators because they are vulnerable to terrestrial and arboreal species (Martin 1993). Finally, we test the prediction that smaller birds should have a more diverse predator assemblage than larger birds.

Data sources and inclusion criteria

We located studies that used nest cameras to identify predators in North America via a literature search in Google Scholar (accessed February 2014). We used the following search terms individually and in combination: "nest," "predation," "predator," "camera," "video," and "videography." We located additional sources from the literature-cited sections in the articles we found and from personal contact with other researchers. We used peer-reviewed articles as well as government reports and theses and dissertations. We also included an unpublished data set from a large-scale shrubland bird nest monitoring study being conducted by the authors in Illinois. Because of the biases associated with using artificial nests to infer predator identity (Thompson and Burhans 2004), we excluded artificial nests from our analyses; we did, however, use data based on real nests from studies monitoring both real and artificial nests. When recent studies included data presented in previously published articles (e.g., Stake and Cimprich 2003, Reidy et al. 2008, Reidy and Thompson 2012), we avoided double sampling nests by extracting data from the most comprehensive studies first and then from preceding articles within the same system. We excluded one large nest-camera study that used predator control, thereby altering the nest-predator community for some nests (Ellis-Felege 2012). However, we chose to include another study that used predator-exclusion fences because the authors found no differences in the predator community between control and treatment nests (Conner et al. 2010).

From each study, we extracted information regarding the location of the study, the nesting characteristics of the focal nesting species, and the fates of each nest monitored with a camera. For each study, we extracted latitude, longitude, and elevation using details provided by the authors or using Google Earth. To assess the influence of the nesting characteristics of the focal bird species, we categorized the nesting habitat, nest-height guild, and body size of each focal bird species. Using details provided by the authors, we categorized nests as occurring in forest, grassland, shrubland, or "other" (e.g., coastal habitat, urban). Although the "other"

category includes disparate habitat types, these habitats were typically represented by only 1–2 studies and could not be analyzed separately. We grouped nest heights into one of three height categories: low (less than 1.1 meter, m), intermediate (1.1 m to 5 m), or high (more than 5 m). We assigned nests to these categories on the basis of details provided in source material or from the relevant *Birds of North America* species accounts (Rodewald 2015). Finally, for the body size of nesting birds, we categorized each nesting species as large (more than 100 g) or small (less than 100 g) on the basis of data provided in the *Birds of North America* species accounts (Rodewald 2015). We also considered the potential influence of nest shape, length of incubation and nestling periods, and development mode (altricial and semialtricial versus semiprecocial and precocial), but these variables were confounded with both nest height and body size (e.g., low nesting species were often large bodied with long incubation periods and precocial young). Therefore, we omitted these additional variables from our analyses. Where a single study monitored nests in multiple habitat types, nest-height categories, or body-size categories, we assigned values to nests in the study on the basis of the level of detail provided. In some cases, this allowed us to associate estimates with specific habitat types and species. In other cases, such as studies in which multiple species were monitored but estimates were aggregated, we assigned categories on the basis of the majority of nests from the study.

From each study, we categorized the fate of each nest monitored with a video camera. We quantified the number of successful and depredated nests and of nonpredator and predator-related failures, and we recorded predator identities to the lowest taxonomic level possible. We designated the fate of each camera-monitored nest as successful, failed because of predation, failed because of other causes (e.g., weather), or unknown (e.g., because of camera malfunction).

For each study site, we determined the nest-predator community richness. This was simply the number of unique predator species recorded depredating nests at a given location (hereafter "observed predator richness"). For many studies, our estimate of observed predator richness likely underestimated the true nest-predator richness because many predators were not identified to the species level (e.g., predator identity reported as "snake"). In such cases, we calculated the minimum number of species documented at a site. For the examination of the geographic trends in predator identity, we defined six nest-predator guilds for analyses: rodents, mesopredators (medium-sized mammalian predators), corvids, raptors, brown-headed cowbirds (*Molothrus ater*), and snakes.

Analyses

We evaluated geographic patterns in predation probability by each of our six predator guilds using a generalized linear mixed model with a multinomial distribution and generalized logit link function (SAS PROC GLIMMIX, SAS Institute 2008; Littell et al. 2006). Our seven response variables included each predator guild ($n = 6$) in addition to an "other fate" category that included successful nests as well as nests failing from causes other than predation, unknown causes, and predation by taxa that did not fall into one of the six predator guilds; this "other fate" category was used as our reference group. Each nest was represented by a separate row in the data; therefore, each study in the analysis was weighted by the sample size of nests. We modeled the influence of the linear and quadratic effects of latitude and longitude, nesting habitat (shrubland, forest, grassland, other), nest-height category (low, intermediate, or high), and bird body-size category (small or large) of each monitored nest. We treated study as a random effect to account for the non-independence of including multiple nests per study. When studies included multiple sites that were widely separated (e.g., different states or provinces) and reported results separately for each location, we treated these as separate studies.

As with traditional nest-survival analyses, focusing on the proportion of nests depredated by various predator groups does not give a true estimate of predator-specific mortality rates. Rather, methods that account for exposure time to generate daily rates of nest predation attributable to different predators would be preferable (e.g., Thompson and Burhans 2003, Thompson and Ribic 2012). Unfortunately, most studies did not present results in enough detail to make this possible. Nonetheless, we have no reason to suspect systematic bias in predator identification on the basis of the way the results of these studies have been presented. Most studies in which nest predation is examined using video technology employ similar procedures, including waiting until incubation to install cameras (to minimize abandonment) and maintaining cameras at nests until fledging or failure, and many researchers prioritize camera installation at incubation rather than nestling-stage nests. Therefore, the results are likely to capture the range of nest predators that are causing nest failures throughout the nesting period and the relative importance of these predators, although any predators that depredate nests during egg laying or early in incubation (e.g., nest parasites) would be underrepresented.

We evaluated geographic patterns in observed predator richness using a generalized linear mixed model (SAS PROC GLIMMIX, SAS Institute 2008; Littell et al. 2006). We used a Poisson distribution with a log link function, used an added term to account for overdispersion, and weighted by the sample size of video-monitored nests. We considered the linear and quadratic effects of latitude and longitude and also included nesting habitat, nest-height category, and bird body-size category. We included the natural logarithm of sample size because of the nonlinear effect of this covariate on observed richness. Therefore, the analyses dealt with uneven sampling, and all predicted values were produced at the mean value for this covariate (i.e., holding sample size constant).

To examine the relationships between predation probability and predator richness, we generated values using the multinomial model above but produced the best linear

unbiased predictors for each study on the basis of the random effect of study site for the groups of predation, survival, and other fate. The latter values were generated using the best linear unbiased predictors from the seven-category multinomial model mentioned below. We then examined the influence of predator richness on total predation probability using a general linear model.

To create maps of the predicted probability of predation by each predator guild and observed predator richness, we used ArcMap 10.1 (ESRI Institute, Redlands, California) to create a grid of 150×150 cells, each approximately 1495 square kilometers in size, that spanned the range of observed latitudes and longitudes for our focal studies. We generated predicted probabilities of predation and observed predator richness for each of these cells using our model that included the additive effects of longitude and the quadratic effect of latitude as well as the effects of bird size, nest-height guild and nesting habitat. The geographic estimates were averaged across bird sizes, nest height guilds, and nesting habitats. We interpolated values using inverse distance weighting and extracted the raster layer generated via our inverse distance weighting to the borders of North America.

Because predator guilds may directly or indirectly interact such that predation from one guild may increase as pressure from another diminishes, we explored the relationships among each of the six predator guilds using Spearman Rank Correlations.

Finally, to examine the relationships between the nesting characteristics of birds and both predator-specific predation and observed predator richness, we used generalized linear mixed models (SAS PROC GLIMMIX, SAS Institute 2008; Littell et al. 2006). For predator-specific predation, we used a multinomial distribution and generalized logit link function, and for richness, we used a Poisson distribution with a log link function and an added term to account for overdispersion. These analyses were weighted by the sample size of video-monitored nests. We specifically tested the effects of nesting habitat (forest, grassland, shrubland, or other), nesting-height guild (low, intermediate, or high), and bird body-size category (small or large) on predator-specific predation and predator richness while also including longitude and the quadratic effect of latitude. For predator richness, we included the natural logarithm of sample size because of the nonlinear effect of this covariate on observed richness. Again, we included study as a random effect to account for the nonindependence of including multiple nests per study. We conducted all analyses in SAS, version 9.2 (SAS Institute, Cary, NC). We considered results significant at $p < 0.05$.

Predator communities

We extracted data from 53 studies that collectively filmed 4208 nests (supplemental appendix S1): 46% (1917 of 4208) of nests with known fates experienced full or partial nest predation, 8% (337 of 4208) failed because of other factors, and 46% (1954 of 4208) were successful. Fate could not be determined for 392 nests because of camera malfunction or other factors. Of all nests filmed, 3512 of the nests (83%) were open cup nests and none were of cavity nesting species.

At least 90 species were identified as nest predators (in numerous cases predators were not identified to species; supplemental appendix 2). Mesopredators (at least 14 species) and snakes (at least 12 species) were the most common nest-predator guilds, accounting for 362 (24%) and 348 (23%) predation events, respectively. Rodents (at least 15 species) accounted for 235 events (15%), raptors (at least 16 species) for 221 events (14%), corvids (at least 7 species) for 134 events (9%), brown-headed cowbirds for 106 events (7%), miscellaneous predators (cervids, passerines, crabs, cattle, etc.) for 78 events (5%), with ants and other invertebrates accounting for 70 predation events (5%; figure 1). Predation was not evenly attributed to all species within predator guilds. The dominant species within guilds were the following: mesopredators, raccoons (*Procyon lotor*: 31% of predation events attributed to mesopredators); snakes, ratsnakes (*Elaphe obsoleta:* 60%); rodents, red squirrels (*Tamiasciurus hudsonicus*: 19%); raptors, Cooper's hawks (*Accipiter cooperii*: 20%); corvids, blue jays (*Cyanocitta cristata*: 29%); and insects, fire ants (*Solenopsis invicta*: 74%).

The observed richness of nest predators documented at a site ranged from 0 to 23 species, with a mean of 8. Observed nest-predator richness was influenced by latitude ($F(1,44) = 14.94$, $p < .001$) and the quadratic effect of latitude ($F(1,44) = 12.67$, $p < .001$) but not longitude ($F(1,44) = 2.18$, $p = .147$), such that the number of predator species observed was greatest at midlatitudes and decreased at high and low latitudes (figure 2).

The natural logarithm of sample size of filmed nests was a significant covariate for nest-predator species richness ($F(1,44) = 62.66$, $p < .001$). Observed predator richness reached an asymptote after approximately 175 nests were filmed or 75 nest-predation events were documented. However, observed predator richness was a poor predictor of total nest-predation probability ($F(1,54) = 0.37$, $p = .544$).

Geographic variation in predation

Overall, predation probability was greatest at low latitudes and decreased at higher latitudes (figure 3). However, predation probability was not geographically uniform among the different predator guilds, because predation varied significantly with latitude ($F(6,3842) = 3.03$, $p = .006$) and the quadratic effect of latitude ($F(6,3842) = 2.97$, $p = .007$) but not longitude ($F(6,3842) = 1.53$, $p = .165$). Predation probability by corvids was greatest in the southwestern United States (figure 4a). Nest-predation probability by mesopredators was greatest at high latitudes, likely driven by the dominance of the Arctic fox (*Vulpes lagopus*) at two study locations. Otherwise, mesopredator predation was uniformly moderate throughout the rest of North America (figure 4b). Nest-predation probability by snakes was greatest in the southeastern region of the continent (figure 4c). Predation probability by rodents peaked in the Western boreal forests
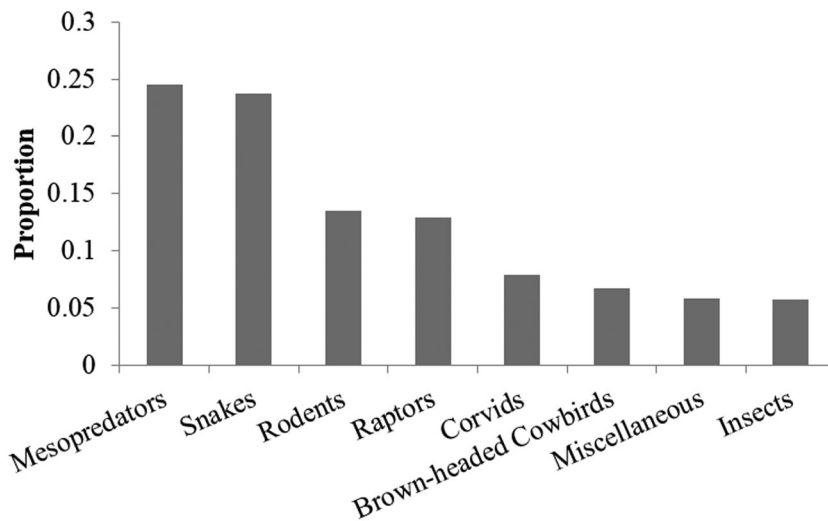
Figure 1. The proportion of known-identity predation events attributed to each major nest-predator guild from 1917 nest-predation events, derived from 53 North American studies using video cameras to identify nest predators.

and Western Great Plains region (figure 4d). No meaningful geographic trends were detected for predation probability by raptors or cowbirds.

We found positive and negative correlations in the geographic variation of predation probability by guilds. As predation probability by snakes declined, depredation probability from rodents increased ($\rho = -0.27$, $p = .042$). Predation probability by both raptors and corvids decreased as predation probability from mesopredators increased ($\rho = -0.53$, $p < .001$ and $\rho = -0.26$, $p = .051$, respectively). Finally, predation probabilities by snakes and cowbirds and by raptors and small mammals were positively related ($\rho = 0.30$, $p = .024$, and $\rho = 0.34$, $p = .010$, respectively).

Influence of nesting characteristics on predation

Observed nest-predator richness did not vary by bird size ($F(1,44) = 0.38$, $p = .543$), nesting habitat ($F(3,44) = 1.57$, $p = .210$), or height ($F(2,44) = 0.30$, $p = .739$; figure 5). Predator-specific predation probabilities were significantly influenced by bird size ($F(6,3842) = 2.62$, $p = .015$), nesting habitat ($F(18,3842) = 3.35$, $p < .001$), and nest-height guild ($F(12,3842) = 2.11$, $p = .014$). Large birds were less likely to be preyed on by cowbirds, snakes, and rodents than small birds were ($\beta = -4.544$, standard error [SE] = 2.46; $\beta = -1.928$, SE = 0.693; and $\beta = -1.182$, SE = 0.672, respectively; figure 6a). Birds that nested low (less than 1.1 m high) were more likely to be preyed on by mesopredators and less likely to be depredated by snakes than those nesting high (i.e., more than 5m; $\beta = 3.859$, SE = 2.178, and $\beta = -1.744$, SE = 0.886, respectively; figure 6b). Intermediate (1.1 m–5 m) and high (more than 5 m) nests were more likely to be preyed on by raptors and rodents than nests low to the ground (raptors: $\beta = 1.618$, SE = 0.545, and $\beta = 2.451$, SE = 0.839; and rodents: $\beta = 0.814$, SE = 0.487, and $\beta = 1.601$,

SE = 0.843, respectively). Regarding habitat patterns, shrubland nests were more susceptible to predation by snakes than nests in forests ($\beta = 1.692$, SE = 0.381; figure 6c), although the susceptibility in shrublands and grasslands was similar ($\beta = 0.702$, SE = 0.625). Corvids more commonly depredated nests in forests than in shrublands ($\beta = 1.066$, SE = 0.50).

Discussion

We reviewed 53 studies that used cameras to monitor more than 4000 nests of North American birds and were able to discern several broadscale trends in predator identity, predator richness, and the nesting characteristics that influenced predator identity and richness. We found that nesting birds faced a wide variety of nest predators (more than 90 species) and that major predator species and predation probability by various nest-predator guilds varied geographically. In addition, predator-specific predation probabilities were influenced by a bird's body size, nesting habitat, and nest height. Below, we discuss the patterns we observed and the potential underlying causes.

Geographic variation in nest predation. Predation by predator guilds varied geographically, a pattern found in a smaller study of nest predation in North America (Thompson and Ribic 2012). More specifically, similar to Thompson and Ribic (2012), we found that snakes and mammals were frequent nest predators in southern and northern locations, respectively. Our results suggest that overall, geographic patterns in predation are driven by the abundance or distribution of particularly dominant nest-predator species within these predator guilds. For instance, higher rates of nest predation by corvids in the Southwest are likely because common ravens (*Corvus corax*) occur in very high densities in areas of the Mojave Desert where they are subsidized by anthropogenic food and water sources (Boarman et al. 2006). The greater probability of nest predation by rodents in the boreal forest and Western Great Plains regions may be a function of the distribution and habitat affinities of two important nest-predator species: the red squirrel and the thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*; appendix S2). Ground squirrels are associated with open grasslands and can be important local predators (Rongstad 1965; Pietz and Granfors 2000), whereas red squirrels are associated with northern conifer forests and are responsible for a large number of nest failures in these habitats (Ball et al. 2008). Nest-predation probability by snakes was greatest in the Southeast, not only where snakes are more diverse (Schall and Pianka 1978) but also where important snake nest-predator species occur. Ratsnakes, the most frequent
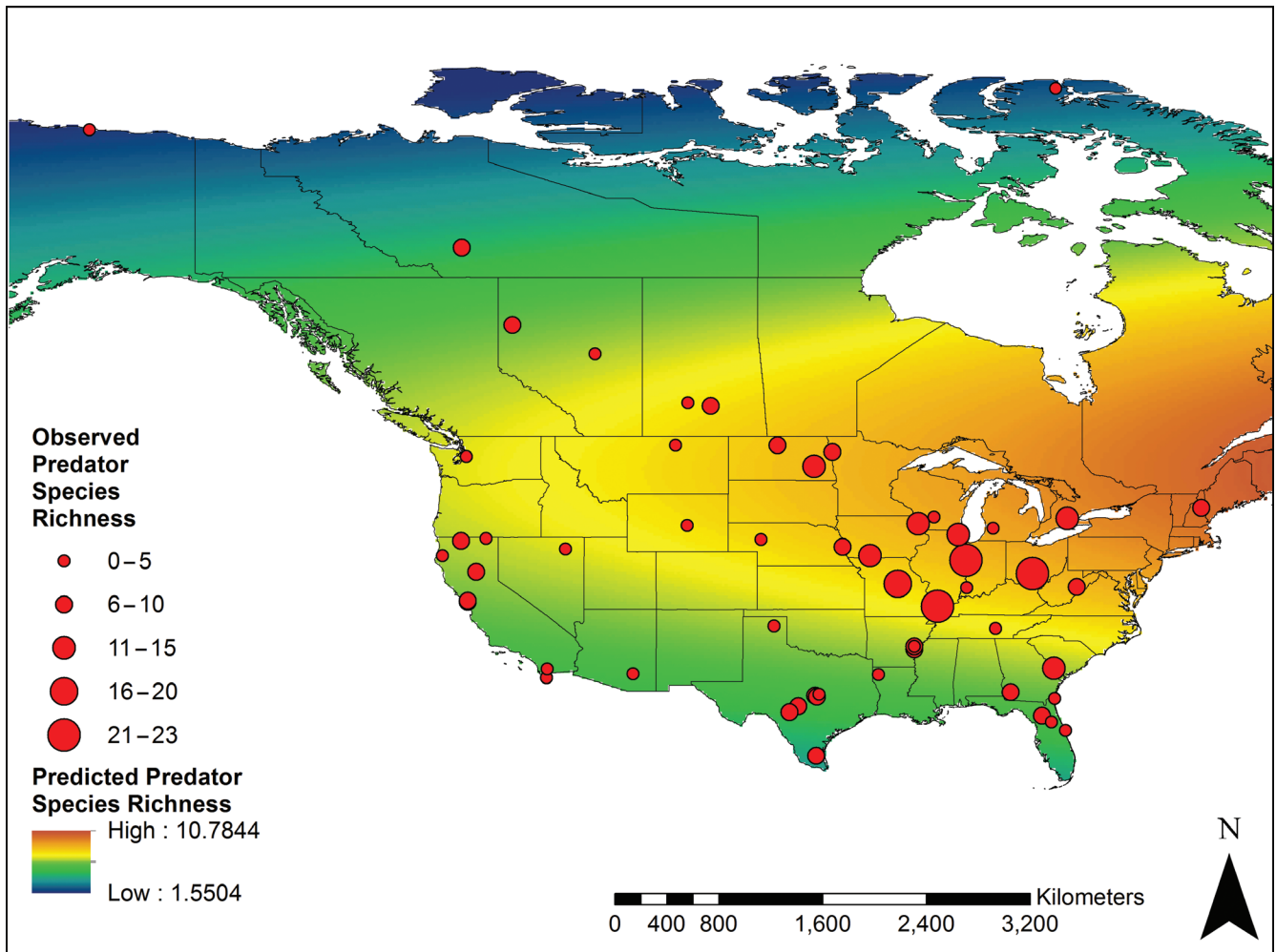
Figure 2. Observed and predicted nest-predator species richness throughout North America. The circles indicate the locations of 53 nest-camera studies, and the size of the circle corresponds with the observed nest-predator richness for that study. The predicted nest-predator richness was estimated via a model including the effects of longitude, the quadratic effect of latitude, the nesting habitat (shrubland, forest, grassland, or other), the nest height category (low, intermediate, or high), and the bird body-size category (less than 100 versus more than 100 grams). The natural logarithm of the sample size of video-monitored nests was included as a covariate.

snake nest predator in North America (DeGregorio et al. 2014a), are a widespread and common species in many southeastern US habitats. For some taxa, such as raptors and cowbirds, there were no clear geographic patterns. We suspect that as more nest-camera studies are conducted, particularly in underrepresented areas (the desert Southwest, the Great Plains, and northeastern North America) or focused on underrepresented bird groups (e.g., cavity and canopy nesters), new patterns may emerge.

Beyond geographic trends in predation, we also identified positive and negative correlations between the predation probabilities of some guilds, which may be the result of several nonmutually exclusive ecological mechanisms. First, different predators may compete with each other, such that nest predation is compensatory at local scales. Indeed, the removal of mesopredators in several past studies has led

to increased nest predation by other guilds and no overall change in predation rates (Dion et al. 1999, Ellis-Felege et al. 2012), although it is unknown whether nest predation is compensatory at larger spatial scales. Second, predation and competition among predator guilds could operate simultaneously to produce the observed patterns. For example, we found that nest-predation probability by rodents was low when nest predation by snakes was high. This may be because some dominant snake species preying on nests also prey extensively on rodents (e.g., ratsnakes; Weatherhead et al. 2003, Carfagno et al. 2006). Therefore, where snakes are abundant, they may outcompete rodents for bird nests, suppress rodent numbers via predation, or alter rodent foraging behavior—or all of these factors could operate simultaneously. Third, positive associations between nest-predation probability by snakes and cowbirds
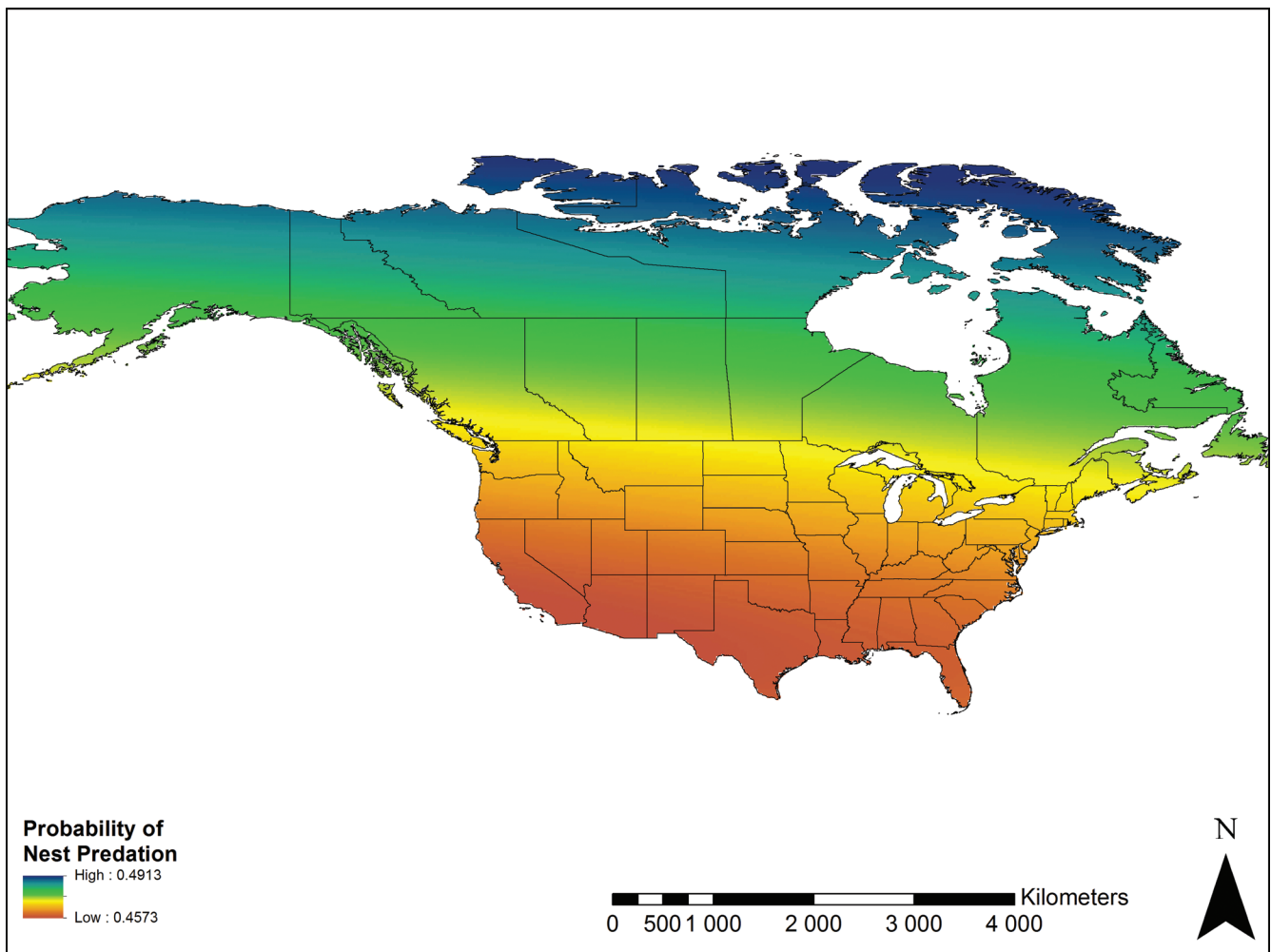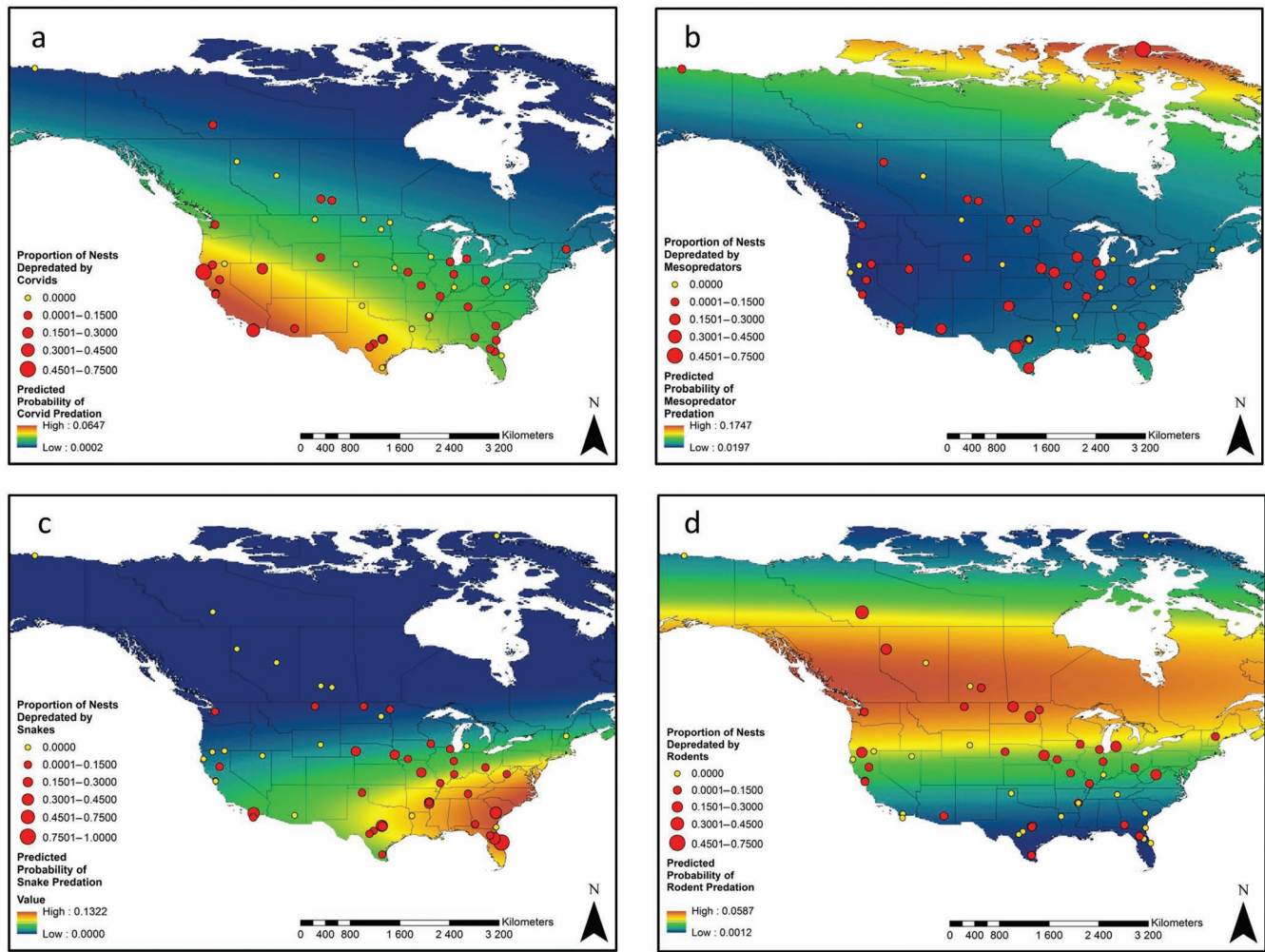
Figure 3. The predicted probability of nest predation based on results from 53 North American nest-camera studies. The nest-predation probability was estimated via a model including longitude, the quadratic effect of latitude, the nesting habitat (shrubland, forest, grassland, or other), the nest-height category (low, intermediate, or high), and the bird body-size category.

and by raptors and rodents could involve both groups independently favoring similar habitats. For example, both cowbirds and many snakes associate with forest-edge habitat (e.g., Blouin-Demers and Weatherhead 2001, Howell et al. 2007) and red squirrels and accipiter raptors prefer to breed in dense, mature forest stands (Reynolds et al. 1982, Boon et al. 2008).

Influence of nesting characteristics on predation. We also found that predator-specific predation probabilities varied on the basis of the nesting characteristics of birds. For instance, snakes were more likely to prey on nests in shrublands and grasslands than forests, similar to the findings of other researchers (Thompson and Burhans 2003, Cox et al. 2012b). This generally reflects both habitat use patterns of predator species and the accessibility of nests to predators. For example, although some snake predators are very arboreal (e.g., ratsnakes; Jackson 1976), others are primarily

terrestrial (e.g., North American racers, *Coluber constrictor*) and are unlikely to prey on nests high in trees. Similarly, most mesopredators are terrestrial foragers and should be much more likely to encounter nests on or near the ground. Conversely, raptors and corvids were much more likely to prey on nests at intermediate or greater heights which likely reflect their vertical distribution within habitats. Many studies have shown differences in nest-predation rates by nest height, although results vary between studies (Filliater et al. 1994, Wilson and Cooper 1998, Siepielski et al. 2001, Colombelli-Negral and Kleindorfer 2009), likely because of the different predatory threats faced by birds nesting at different heights. Taken collectively, the geographic and nest-height patterns in predator-specific predation we found may help clarify why predation patterns vary. In fact, our results show the importance of rodents for high or intermediate nests relative to low nests, likely reflecting the importance of arboreal squirrels. We suggest that broad patterns of

Figures 4. The predicted predator-specific nest-predation probabilities across North America for (a) corvids, (b) mespredators, (c) snakes, and (d) rodents. The nest-predation probability for each guild was estimated via a model including longitude, the quadratic effect of latitude, the nesting habitat (shrubland, forest, grassland, or other), the nest-height category (low, intermediate, or high), and the bird body-size category.

geographic variation in nest survival of bird species may be influenced by geographic variation in nest-predator identity.

Predator richness. We hypothesized that the probability of nest predation would increase as predator richness increased because it may be difficult for birds to nest or behave in ways that reduce the risk from all predators simultaneously (e.g., Filliater et al. 1994). Alternatively, when only one type of predator is dominant, perhaps those predators are better able to specialize and become more effective nest predators. Although predator species richness varied geographically, generally decreasing at higher latitudes, we did not detect a relationship between nest-predator richness and total nest-predation probability. Therefore, it is likely that predator richness is less important than the local abundance of important predators. For example, although 12 species of snakes have been documented preying on nests, ratsnakes accounted for 60% of all nest predation by snakes. Likewise,

Cooper's hawks, blue jays, raccoons, and red squirrels each accounted for 23%–34% of nest predation attributed to their respective predator guilds. Even species such as the Arctic fox, which were infrequent predators overall, were locally important predators (Liebezeit and Zach 2008, McKinnon and Bêty 2009). Unfortunately, estimating local and regional species abundance is logistically difficult, particularly for secretive species (e.g., snakes) or species whose yearly fluctuations in abundance may alter their impact on nest predation (e.g., rodents and some raptors; Krebs and Berteaux 2006).

In addition to influencing predator-specific predation probabilities, we predicted that nesting characteristics (i.e., habitat, nest height, body size) would influence observed predator richness. Specifically, we predicted that if particular predator species or guilds are associated with forests versus grasslands or are strictly terrestrial versus arboreal, then nests in transitional zones (shrubland or intermediate nest
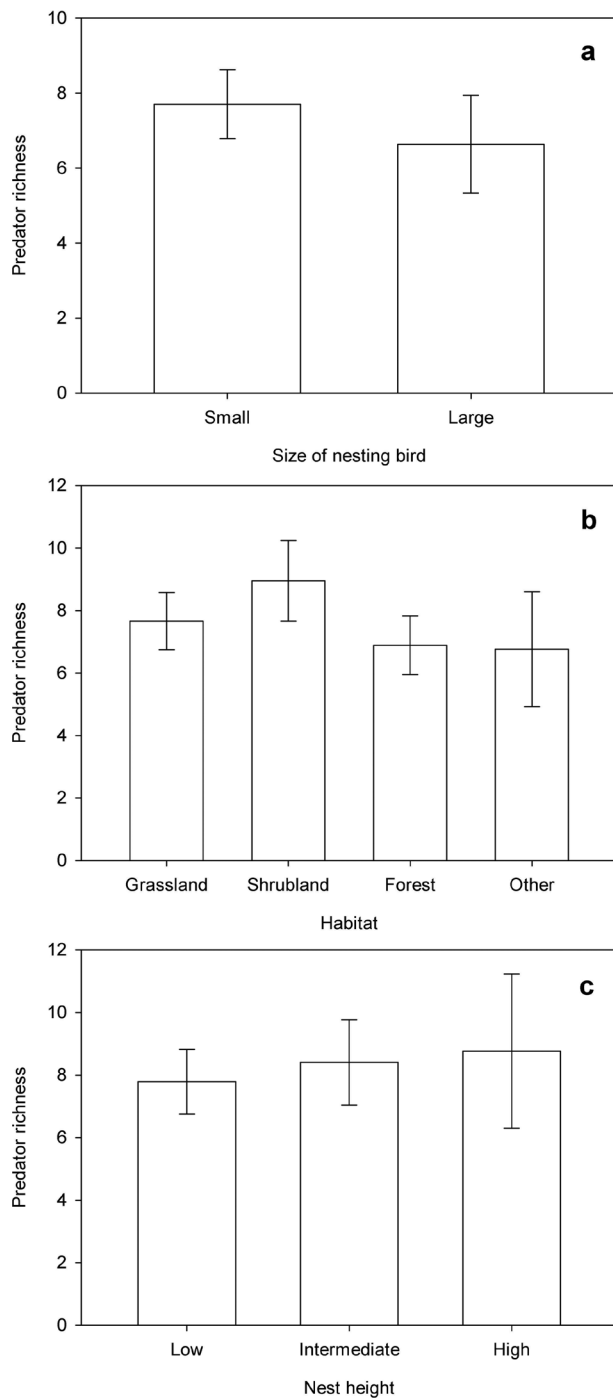
Figure 5. The influence of (a) bird body size (A; small: less than 100 grams), (b) nesting habitat, and (c) nest height (low: less than 1.1 meters, m; intermediate: 1.1 m to 5 m; high: more than 5 m) on the minimum number of predator species observed depredating nests in 53 North American studies using video cameras to identify nest predators. The bars represent standard errors.

heights) would experience greater predation rates. However, our results did not support these predictions, and neither nesting habitat nor height had any effect on observed nest-predator richness. Similarly, we found no evidence that

smaller birds were at risk from a larger array of predator species than larger birds.

Implications for nesting birds

Geographic variation in which nest predators are important generates interesting questions regarding how widespread bird species respond to variability in predator-specific predation. For example, although nest-site selection is expected to evolve to minimize the risk of nest predation (Latif et al. 2012), our results indicated that bird species with broad distributions were likely to confront a range of nest predators that employ different foraging strategies. Therefore, nest-site selection that is adaptive in one part of a species' range may be maladaptive elsewhere. The behavior of one relatively widespread species, the orange-crowned warbler (*Oreothlypis celata*), illustrates the capacity of some birds to radically shift the location of their nests in response to changes in predation risk (Peluc et al. 2008). Although some species appear incapable of shifting their nest location in response to predation risk (Fontaine et al. 2007), the ability to do so should be more prevalent in wide-ranging species exposed to geographically variable predator communities.

Implications for researchers

Our analyses revealed several limitations of the available data, ways to improve on future studies, and opportunities for future research. The studies we reviewed here varied in their scope, scale, and goals, which naturally resulted in a number of inconsistencies among studies. First, sampling has been uneven geographically. Few nest-camera studies have been conducted in the desert Southwest, Mexico, the northeastern United States, northeastern Canada, or central Canada, limiting our ability to accurately predict guild-specific nest-predation probabilities in these regions. Data from these areas are needed to confirm or refute some of our extrapolations and thereby improve the accuracy of geographic models of predator communities and predation risk. In addition, over 80% of the nests filmed for this study were open-cup nests, resulting in a biased sample that lacked cavity nests. Second, the precision with which nest predators were identified varied among studies. Although this is likely a consequence of difficulty in identifying oftentimes-blurry images of predators, greater consultation with taxonomic experts may improve predator identification. Third, we know relatively little about some nesting habitats. For example, most studies have focused on ground- or shrub-nesting species, presumably because of the difficulties of finding and filming canopy nests. As a result, our knowledge of canopy-nest-predator communities lags behind that of other nesting guilds (e.g., Chiavacci et al. 2014). Finally, we realize that it is difficult to obtain larger sample sizes under many circumstances. However, studies that monitor more nests give a more comprehensive view of nest-predator communities (Weidinger 2008). Hopefully, as the price and size of video-monitoring equipment continues to decrease, it will be more
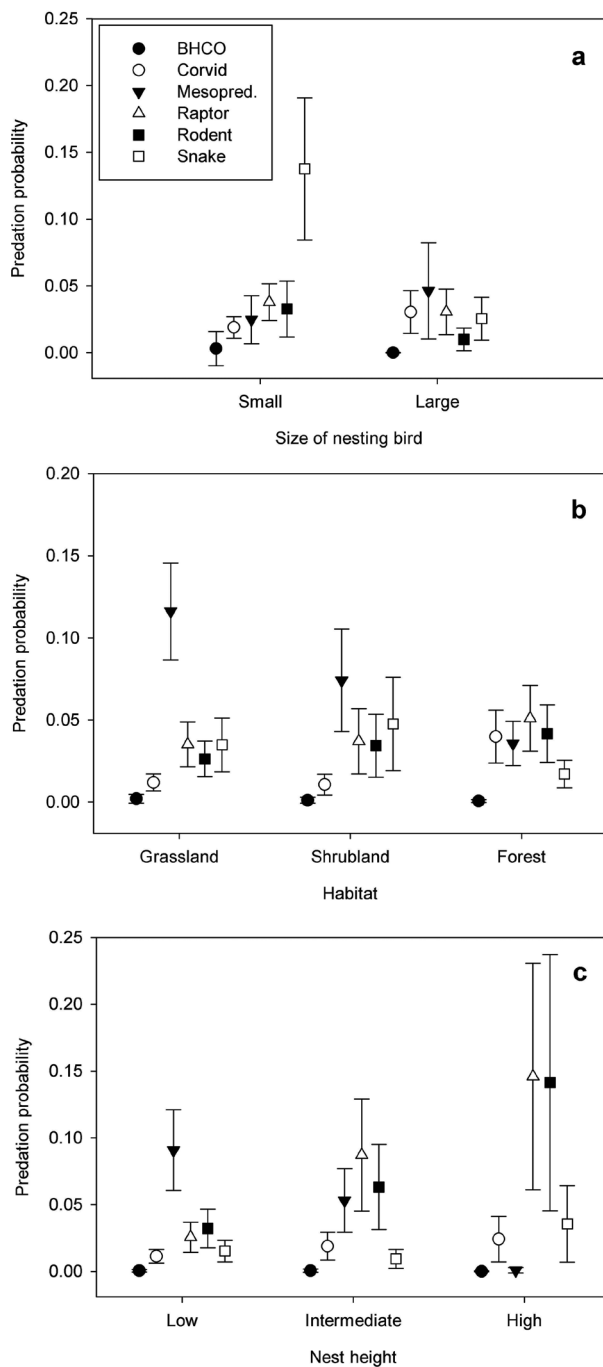
Figure 6. The influence of body size, nesting habitat, and nest height on predator-specific predation probability among 53 North American studies using video cameras to identify nest predators. The estimates for (a) are based on the average of all the habitat and height categories; the estimates for (b) and (c) were generated on the basis of the average across small and large birds and on the basis of the proportional representation of nests of each height category found in each habitat type (e.g., 10%, 90%, and 0% of nests in grassland; 26%, 74%, and 0% of nests in shrubland; and 36%, 57%, and 7% of nests in forest were assigned to low, intermediate, and high nesting classes, respectively). The error bars represent standard errors.

feasible for more studies to increase their sampling efforts (Cox et al. 2012a).

Supplemental material
The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biw071/-/DC1*.

References cited
Bader TJ, Bednarz JC. 2009. Reproductive success and causes of nest failures for Mississippi kites: A sink population in eastern Arkansas? Wetlands 29: 598–606.

Ball JR, Bayne EM, Machtans CS. 2008. Energy sector edge effects on songbird nest fate and nest productivity in the boreal forest of western Canada: A preliminary analysis. Tundra to Tropics 4: 13–16.

Benson TJ, Brown JD, Bednarz JC. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79: 225–234.

Blouin-Demers G, Weatherhead PJ. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 82: 2882–2896.

Boarman WI, Patten MA, Camp RJ, Collis SJ. 2006. Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. Journal of Arid Environments 67: 248–261.

Boon AK, Reale D, Boutin S. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. Oikos 117: 1321–1328.

Carfagno GL, Heske EJ, Weatherhead PJ. 2006. Does mammalian prey abundance explain forest-edge use by snakes? Ecoscience 13: 293–297.

Chalfoun AD, Ratnaswamy MJ, Thompson FR III. 2002. Songbird nest predators in forest–pasture edge and forest interior in a fragmented landscape. Ecological Applications 12: 858–867.

Chiavacci SJ, Bader TJ, Bednarz JC. 2014. Preferred nest site characteristics reduce predator-specific predation risk in a canopy nesting raptor. Journal of Wildlife Management 78: 1022–1032.

Colombelli-Negral D, Kleindorfer S. 2009. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). Ecological Research 24: 921–928.

Conner ML, Rutledge JC, Smith LL. 2010. Effects of mesopredators on nest survival of shrub-nesting songbirds. Journal of Wildlife Management 74: 73–80.

Cox WA, Pruett MS, Benson TJ, Chiavacci SJ, Thompson FR III. 2012a. Development of camera technology for monitoring nests. Studies in Avian Biology 43: 185–198.

Cox WA, Thompson FR III, Faaborg J. 2012b. Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. Auk 129: 147–155.

———. 2012c. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landscape Ecology 27: 659–669.

Cox WA, Thompson FR III, Reidy JL. 2013. The effects of temperature on nest predation by mammals, birds, and snakes. Auk 130: 1–7.

Dion N, Hobson KA, Larivière S. 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. Canadian Journal of Zoology 77: 1801–1806.

DeGregorio BA, Chiavacci SJ, Weatherhead PJ, Willson JD, Benson TJ, Sperry JH. 2014a. Snake predation on North American bird nests: Culprits, patterns, and future directions. Journal of Avian Biology 45: 325–333.

DeGregorio BA, Weatherhead PJ, Sperry JH. 2014b. Powerlines, roads, and avian nest survival: Effects on predator identity and predation intensity. Ecology and Evolution 4: 1589–1600.

Dijak WD, Thompson FR III. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64: 209–216.

Ellis-Felege SN, Conroy MJ, Palmer WE, Carroll JP. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. Journal of Applied Ecology 49: 661–669.

Filliater TS, Breitwisch R, Nealen PM. 1994. Predation on northern cardinal nests: Does choice of nest site matter? Condor 96: 761–768.

Fontaine JJ, Martel M, Markland HM, Niklison AM, Decker KL, Martin TE. 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116: 1887–1894.

Howell CA, Dijak WD, Thompson FR III. 2007. Landscape context and selection for forest edge by breeding brown-headed cowbirds. Landscape Ecology 22: 273–284.

Jackson JA 1976. Relative climbing tendencies of gray (*Elaphe obsoleta spiloides*) and black rat snakes (*E. o. obsoleta*). Herpetologica 32: 359–361.

Klug PE, Jackrel SL, With KA. 2010. Linking snake habitat use to nest predation risk in grassland birds: The dangers of shrub cover. Oecologia 162: 803–813.

Krebs CJ, Berteaux D. 2006. Problems and pitfalls in relating climate variability to population dynamics. Climate Research 32: 143–149.

Latif QS, Heath SK, Rotenberry JT. 2012. How avian nest site selection responds to predation risk: Testing an "adaptive peak hypothesis." Journal of Animal Ecology 81: 127–138.

Liebezeit JR, George TL. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. Condor 104: 507–517.

Liebezeit JR, Zack S. 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.

Littell RC, Stroup WW, Milliken GA, Wolfinger RD, Schabenberger O. 2006. SAS for Mixed Models. SAS Institute.

Martin TE. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? Ecology 69: 74–84.

———. 1993. Nest predation and nest sites. BioScience 43: 523–532.

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

Montgomerie RD, Weatherhead PJ. 1988. Risks and rewards of nest defence by parent birds. Quarterly Review of Biology 63: 167–187.

Peluc SI, Sillett TS, Rotenberry JT, Ghalambor CK. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19: 830–835.

Peterson BL, Kus BE, Deutschman DH. 2004. Determining nest predators of the Least Bell's Vireo through point counts, tracking stations, and video photography. Journal of Field Ornithology 75: 89–95.

Pietz PJ, Granfors DA. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 2000: 71–87.

———. 2005. Parental nest defense on videotape: More reality than myth. Auk 122: 701–705.

Reidy JL, Thompson FR III. 2012. Predatory identity can explain nest predation patterns. Studies in Avian Biology 43: 135–148.

Reidy JL, Stake MM, Thompson FR III. 2008. Golden-cheeked warbler nest mortality and predators in urban and rural landscapes. Condor 110: 458–466.

Reynolds RT, Meslow EC, Wight HM. 1982. Nesting habitat of coexisting Accipiter in Oregon. Journal of Wildlife Management 46: 124–138.

Ricklefs RE. 1969. An analysis of nesting mortality in birds. Smithsonian Contribution to Zoology 9: 1–48.

Robinson SK, Wilcove DS. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. Bird Conservation International 4: 233–249.

Rodewald P, ed. 2015. The Birds of North America Online. Cornell Laboratory of Ornithology. (10 May 2016; *http://bna.birds.cornell.edu/BNA*)

Rongstad OJ. 1965. A life history study of thirteen-lined ground squirrels in southern Wisconsin. Journal of Mammalogy 46: 76–87.

Schall JJ, Pianka ER. 1978. Geographical trends in numbers of species. Science 201: 679–686.

Siepielski AM, Rodewald AD, Yahner RH. 2001. Nest site selection and nesting success of the red-eyed vireo in central Pennsylvania. Wilson Bulletin 113: 302–307.

Söderström B, Pärt T, Rydén J. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: An experiment and a review. Oecologia 117: 108–118.

Sperry JH, Peak RG, Cimprich DA, Weatherhead PJ. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39: 379–383.

Sperry JH, Cimprich DA, Peak RG, Weatherhead PJ. 2009. Is nest predation on two endangered bird species higher in habitats preferred by snakes? Ecoscience 16: 111–118.

Stake MM, Cimprich DA. 2003. Using video to monitor predation at black-capped vireo nests. Condor 105: 348–357.

Thompson FR III, Burhans DE. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 2003: 408–416.

———. 2004. Differences in predators of artificial and real songbird nests: Evidence of bias in artificial nest studies. Conservation Biology 18: 373–380.

Thompson FR III, Ribic CA. 2012. Conservation implications when nest predators are known. Studies in Avian Biology 43: 23–33.

Thompson FR III, Dijak WD, Burhans DE. 1999. Video identification of predators at songbird nests in old fields. Auk 116: 259–264.

Weatherhead PJ, Blouin-Demers G. 2004. Understanding avian nest predation: Why ornithologists should study snakes. Journal of Avian Biology 35: 185–190.

Weatherhead PJ, Blouin-Demers G, Cavey KM. 2003. Seasonal and prey-size dietary patterns of black ratsnakes (*Elaphe obsoleta obsoleta*). American Midland Naturalist 150: 275–281.

Weatherhead PJ, Carfagno GLF, Sperry JH, Brawn JD, Robinson SK. 2010. Linking snake behavior to nest predation in a Midwestern bird community. Ecological Applications 20: 234–241.

Weidinger K. 2008. Identification of nest predators: A sampling perspective. Journal of Avian Biology 39: 640–646.

Wilson RR, Cooper RJ. 1998. Acadian flycatcher nest placement: Does placement influence reproductive success? Condor 1998: 673–679.

Brett A. DeGregorio (badegregorio@gmail.com), Scott J. Chiavacci, Thomas J. Benson, Jinelle H. Sperry, and Patrick J. Weatherhead are affiliated with the Department of Natural Resources and Environmental Sciences at the University of Illinois, in Champaign–Urbana. BAD and JHS are also with the Engineer Research and Development Center, in Champaign, Illinois. SJC and TJB are affiliated with the Illinois Natural History Survey of the Prairie Research Institute at the University of Illinois, in Champaign–Urbana.