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Effects of Climate and Exurban Development on Nest Predation and Predator Presence in the southern Appalachian Mountains (U.S.A.)

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Abstract: *In the eastern United States, land-use and climate change have likely contributed to declines in the abundance of Neotropical migrant birds that occupy forest interiors, but the mechanisms are not well understood. We conducted a nest-predation experiment in southern Appalachian Mountain forests (North Carolina, U.S.A.) during the 2009 and 2010 breeding seasons to determine the effects of exurban development and temperature on predator presence and the average number of days until eggs in an artificial nest were disturbed by predators. We baited artificial nests with quail (*Excalfactoria chinensi*) eggs and monitored them for 18 days. We used clay eggs, track plates, and motion-triggered cameras to detect and identify nest predators. The average number of days a nest was undisturbed decreased as mean temperature increased and, to a lesser extent, as the density of buildings increased. Nests on the ground were more often depredated than those in trees, likely due to increased predation by opossum (*Didelphis virginiana*) and other carnivores. Raccoons (*Procyon lotor*), opossums, corvids (*Corvus brachyrhynchos and Cyanocitta cristata*), chipmunks (*Tamias striatus*), black bears (*Ursus americanus*), and domestic cats (*Felis catus*) were the most commonly detected predators. Presence of these predators did not vary as a function of mean temperature. Domestic cats and corvids were detected more frequently in plots with high rather than low densities of buildings. Forest-interior specialists and Neotropical migrants often nest in cool, high-elevation areas with low housing density. These bird species, especially those that nest on the ground, may be most vulnerable to increased nest predation if temperature and exurban development increase at higher elevations as anticipated.*

Keywords: artificial nests, Blue Ridge Mountains, clay eggs, elevation, land use, motion-triggered cameras, track plates

Efectos del Clima y el Desarrollo Exurbano sobre la Depredación de Nidos y la Presencia de Depredadores en el Sur de las Montañas Apalaches (E.U.A.)

Resumen: *En el este de Estados Unidos, es probable que el uso de suelo y el cambio climático han contribuido a declinaciones en la abundancia de aves migratorias neotropicales que ocupan el interior de bosques, pero los mecanismos no son bien comprendidos. Realizamos un experimento de depredación de nidos en bosques del sur de las Montañas Apalaches (Carolina del Norte, E. U. A.) durante las épocas reproductivas de 2009 y 2010 para determinar los efectos del desarrollo exurbano y la temperatura sobre la presencia de depredadores y el número promedio de días hasta que los huevos en un nido artificial fueron perturbados por depredadores. Cebamos los nidos artificiales con huevos de codorniz (*Excalfactoria chinensi*) y los monitoreamos durante 18 días. Utilizamos huevos de plastilina, placas para huellas y cámaras sensibles al movimiento para detectar e identificar depredadores de nidos. El número promedio de días que un nido no era perturbado disminuyó conforme aumentó la temperatura promedio y, en menor grado, a medida que aumentó la densidad de edifi-*

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cios. Los nidos sobre el suelo fueron depredados más a menudo que los colocados en árboles, probablemente debido al incremento de depredación por zarigüeyas (*Didelphis virginiana*) y otros carnívoros. Mapaches (*Procyon lotor*), zarigüeyas, córvidos (*Corvus brachyrhynchos y Cyanocitta cristata*), ardillas (*Tamias striatus*), osos negros (*Ursus americanus*) y gatos domésticos (*Felis catus*) fueron los depredadores más detectados. La presencia de estos depredadores no varió como una función de la temperatura promedio. Los gatos domésticos y córvidos fueron detectados más frecuentemente en parcelas con densidad alta de edificios. Los especialistas de interior de bosque y los migrantes neotropicales a menudo anidan en áreas frescas y altas con densidad baja de viviendas. Estas especies de aves, especialmente las que anidan sobre el suelo, pueden ser más vulnerables a una mayor depredación de nidos si la temperatura y el desarrollo exurbano aumentan en elevaciones altas como se prevee.

Palabras Clave: cámaras sensibles al movimiento, elevación, huevos de plastilina, Montañas Blue Ridge, nidos artificiales, placas para huellas, uso de suelo

Introduction

Many bird species have declined in abundance in the deciduous forests of eastern North America, especially forest-interior specialists and Neotropical migrants (Sauer & Link 2011). Changing patterns of land use and climate may be contributing to these declines. Exurban development (low-density rural residential and urban-fringe development) is one of the fastest growing forms of land use in the United States (Brown et al. 2005; Hansen et al. 2005). Low-density housing in forested habitat decreases the diversity and abundance of Neotropical migrant bird species (Friesen et al. 1995). The mechanisms responsible for decreases in Neotropical migrants as low-density housing increases are not well understood, and less is known about how climate change may affect the way birds respond to various levels of housing density.

Nest predation has a large effect on the population sizes of birds, especially Neotropical migrants and forest-interior species (Wilcove 1985). Most nest failures are associated with predation (Ricklefs 1969), which has been the subject of many studies. Nevertheless, understanding of the factors that influence nest predation is incomplete. Landscape and local habitat characteristics such as vegetation type and structure influence nest predation indirectly by altering the occurrence and abundance of predator species (Bayne et al. 1997; Dijak & Thompson 2000; Sinclair et al. 2005) or the ability of predators to locate nests (Farnsworth & Simons 1999; Chalfoun & Martin 2009). Given the recent rise in exurban development, we sought to understand how residential development may affect rates of nest predation and nest predators (Fraterrigo & Wiens 2005). Climate change is also likely to affect nest predation by altering the distribution and abundance of nest predators. Exurban development and climate change may interact in unexpected ways; therefore, we examined how exurban development and mean temperature affect nest predation and the presence of nest predators.

Thorington and Bowman (2003) suggest nest predation increases as exurban development increases. This process may be mediated by landscape-level changes in vegetation cover, such as forest fragmentation, and by changes in habitat characteristics. Forest fragmentation often increases nest predation (Paton 1994; Lampila et al. 2005), and exurban development results in fragmentation of forests by roads and houses. Construction of houses may also change the type and structure of surrounding forest vegetation, which alters rates of nest predation (Borgmann & Rodewald 2004). Altered landscape and habitat characteristics are likely to result in changes to predator populations (Nour et al. 1993; Dijak & Thompson 2000). Humans introduce domestic predators, such as cats (*Felis catus*) and dogs (*Canis lupus familiaris*), that prey directly on nests (Lepczyk et al. 2003) or modify the size (Courchamp et al. 1999) and occupancy patterns (Lenth et al. 2008) of populations of natural predators.

In the southern Appalachian Mountains (North Carolina, U.S.A.), climate change may further increase nest predation, especially for forest-interior specialists and Neotropical migrants that nest at high elevations. The southern Appalachian Mountains have a wide range in elevation, and, as in all mountain ranges, mean temperature decreases as elevation increases (Bolstad et al. 1998). In western North America and the tropics predation declines as elevation increases (Hansen & Rotella 2002; Boyle 2008), and this is likely to be true in the southern Appalachian Mountains as well. Temperature-sensitive predators, such as snakes and opossum (*Didelphis virginiana*), may be less active and less abundant at high elevations. Climate in the southeastern United States is projected to become warmer and drier (Mearns et al. 2003). Increases in temperature are associated with shifts in the ranges of many species to higher elevations (Parmesan 2006), and nest predators may be affected similarly.

Exurban development is increasing rapidly in this region, primarily at elevations above 1000 m (Wear & Bolstad 1998; Gragson & Bolstad 2006). In the future, forest-interior and Neotropical migrant species at high elevations may be exposed to nest-predation pressures similar to those experienced by birds at low elevations or in areas with more exurban development. Understanding how nest predation varies along existing gradients of exurban development and mean temperature will provide valuable information about how nest predation may change as exurban development and temperature increase. Furthermore, understanding how abundance of predator species varies in response to current levels of exurban development and temperature may reveal mechanisms underpinning differences in nest predation and provide a basis for strategies to enhance conservation of forest birds.

We used artificial nests and identified predators to examine the effects of building density and mean temperature on nest survival (defined here as the average number of days until eggs placed in an artificial nest were disturbed by predators). We hypothesized that nest survival decreases as building density and mean temperature increase and that the identity and number of predator detections varies as a function of the height of the nest, building density, and mean temperature.

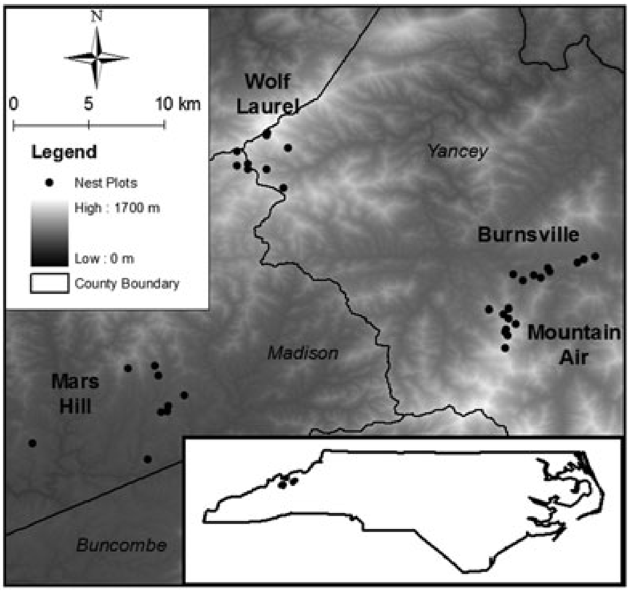

Figure 1. Location and range of elevation (m) of 36 plots located in 4 study sites in the Southern Blue Ridge Province of the southern Appalachian Mountains in North Carolina (inset) (U.S.A.) (bold type, study sites; italics, counties).

Methods

Study Areas

The southern Blue Ridge Physiographic Province in western North Carolina (U.S.A.) is dominated by secondary forest, and forest type and climate vary as a function of elevation, slope, and aspect (Whittaker 1956; Bolstad et al. 1998). Elevation ranges from 380 to 2037 m asl. Forest types are part of the southern Appalachian oak-chestnut region described by Braun (1950) and Stephenson et al. (1993). Species composition of plants varied along the elevation gradient. At low elevations, dominant overstory trees included oaks (*Quercus alba*, *Quercus prinus*, *Quercus rubra*, *Quercus velutina*), red maple (*Acer rubrum*), tuliptree (*Liriodendron tulipifera*), hickory (*Carya glabra*, *Carya tomentosa*, *Carya cordiformis*), American beech (*Fagus grandiflora*), black gum (*Nyssa silvatica*), sweet birch (*Betula lenta*), Eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*). Sourwood (*Oxydendrum arboreum*) and flowering dogwood (*Cornus florida*) were common in the understory. At high elevations, the diversity of overstory trees was lower, and red oaks (*Q. rubra*), American beeches, sugar maples (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*) were dominant. A transition zone occurred between mixed-hardwood forest and northern hardwood forests at 1200 m asl (White et al. 1993). Some ericaceous shrubs (*Kalmia latifolia*, *Rhododendron maximum*) were present at all elevations.

Bird communities were diverse in the study area, and large expanses of forest at high elevations provide breeding habitat for several species of forest-interior specialists and Neotropical migrants (Haney et al. 2001). Common species include Black-throated Blue Warbler (*Dendroica caerulescens*), Black-throated Green Warbler (*Dendroica virens*), Veery (*Catharus fuscescens*), and Blue-headed Vireo (*Vireo solitarius*). Common nest predators include birds (American Crows [*Corvus brachyrhynchos*] and Blue Jays [*Cyanocitta cristata*]), mammals (raccoons [*Procyon lotor*], opossums, black bears [*Ursus americanus*], striped skunks [*Mephitis mephitis*], eastern gray squirrels [*Sciurus carolinensis*], American red squirrels [*Tamiasciurus hudsonicus*], eastern chipmunks [*Tamius striatus*], and weasels [*Mustela* spp.]), and black rat snakes (*Pantherophis obsoletus*) (Farnsworth & Simons 2000).

We positioned nest-predation plots ($n = 36$, 20 × 80 m plots) about 20–40 m from roads in forested areas of at least 0.3 ha. We distributed plots among 4 study areas ($n = 9$ plots/study area) in small towns or residential developments (Wolf Laurel, Mountain Air, Mars Hill, and Burnsville). We selected study areas that had similar ranges in building density that spanned rural (<0.06 buildings/ha) to exurban (0.06–2.50 buildings/ha) development as defined by Brown et al. (2005), but that had different elevation ranges. Plots in Wolf Laurel and Mountain Air were >1100 m asl, and plots in Mars Hill and Burnsville were <900 m asl (Fig. 1). We used a color aerial image to select plot locations that spanned the gradient of building density in each study area (0–1.9 buildings/ha within 200 m of the plot). To calculate the building density of each plot, we digitized each building location that was visible on the aerial image within 200 m of the plot. Images were taken in 2005 and 2006, and we obtained them from mapping departments in Yancey and Madison

Counties. Plots were separated by at least 250 m. All plots were on private property, and before we began sampling we obtained permission from landowners to conduct this research on their land.

Nest Survival and Nest-Predator Identification

We positioned artificial nests ($n = 10$ per plot) 20 m apart along 2 parallel 80-m transects separated by 20 m. If a forest fragment could not accommodate an 80 × 20 m rectangle, we adjusted the arrangement of the nests but kept them 20 m apart. Artificial nests had an average diameter of 107.6 mm (SE 0.4), average depth of 48.4 mm (0.5), and were composed of twigs. We alternated nests between ground and tree (1–2 m high) positions and secured nests to trees with green plastic-coated wire. We baited nests with 2 quail eggs in 2009 on the 21st or 22nd of June and with 1 quail egg and 1 clay egg in 2010 on the 15th or 16th of June and checked nests every 3 days for 18 days. We used eggs of Chinese Blue Breasted Quail (*Excalfactoria chinensis*), which are on average 24.2 mm long (SE 0.2) and 19.5 mm (0.1) wide. These eggs better approximated the size of most songbird eggs than larger Japanese Quail (*Coturnix japonica*) eggs, which are often used in nest-predation studies. We formed clay eggs of similar dimensions with Plastalina modeling clay and tethered them inside artificial nests with thin green wire. To minimize human scent, we wore rubber gloves when handling nests or eggs and plastic gaiters when in the plots. We approached nests from different angles at each visit to avoid leaving a trail.

We measured slope, aspect, and vegetation structure of each plot. We used aspect as a measure of topographic exposure to the southwest by transforming aspect (θ) to an insolation-index value (I) (Beers et al. 1966): $I = \cos[(22.5-\theta) \times \pi/180] + 1$, where 22.5° (northeast) is the lowest value of insolation. We assessed percent visibility of each nest from 3 m to the north, south, east, and west. We used a Braun–Blanquet scale to estimate percent cover of deciduous and evergreen vegetation within 3 m of each nest (0, absent; 1, $\leq$5%; 2, >5–25%; 3, >25–50%; 4, >50–75%; 5, >75–90%; 6, >90%) for 4 vertical layers: herbaceous ($\leq$0.5 m high), shrub (>0.5–3 m), subcanopy (>3–5 m), and canopy (>5 m). We averaged values of nest-visibility and vegetation variables across all nests of the same height in each plot for each year. We used factor analyses to determine which vegetation variables captured most of the plot-level variability in vegetation structure. These analyses included percent cover of deciduous and evergreen vegetation in the 4 vertical layers (8 variables). The first 4 eigenvalues of the correlation matrix were >1.0, so we extracted 4 factors and calculated scores with Bartlett's weighted least-squares method. These factors described variation in deciduous canopy, deciduous subcanopy, evergreen canopy, and evergreen shrub. We eliminated evergreen canopy because it was correlated with other predictor variables.

Mammalian Predator Presence

We used track plates (pieces of foam on which animals tracks make an impression) at all 36 plots and motion-triggered cameras at 12 plots to detect nest predators. We used a method similar to that of Hooper and Rea (2009) to construct track plates from Biofoam (Smithers Bio-Medical Systems, Kent, Ohio). We made track plates from 8 sheets of 15 × 35 cm foam sliced 0.7–1 cm thick. We cut wood siding into 60 × 80 cm sheets and nailed 3 1 × 1 × 60 cm parallel wood strips to the exterior side of the siding sheet 35 cm apart. We placed the foam sheets in the spaces between the wood strips and secured them by wrapping duct tape around the track plate at the locations of the 3 parallel wood strips. We deployed 2 track plates (60 m apart between the 2 nest transects) in all plots in July 2010 (after the nest-predation experiment) and left them for 3 days, after which we removed them. After 4 days, we deployed new track plates for 3 days. We repeated the cycle of deployment and removal 3 times. We baited track plates with 3 small pieces of salmon-flavored cat food to lure nearby mammals to track plates. During the nest-predation experiment, we placed 2 cameras with infrared motion sensors and night-vision flash in 12 plots (Trophy camera, Bushnell Outdoor Products, Overland Park, Kansas). One camera in each plot monitored a ground nest and the other a tree nest.

Exurban Development and Mean Temperature

We used 2008 Google Earth aerial images to view buildings within 200 m of each plot center. We counted the number of houses and buildings that were used intensively (e.g., churches and stores) and converted this count to buildings per hectare. We measured temperature in each plot with iButton (model DS192G, Maxim Integrated Products, Sunnyvale, California) data loggers programed to record temperature hourly during the nest-predation experiment in 2009 and 2010. We used the hourly temperatures to calculate the average daily mean temperature during the breeding season for each plot every year. Average temperatures ranged from 14.7 °C to 22.9 °C (mean = 19.5 °C).

Analyses

We used the average number of exposure days per nest, calculated with Mayfield's (1975) method, to measure nest survival. The number of exposure days for one nest was equal to the number of days during the 18-day nest-predation study until the nest was disturbed by predators. Values ranged from 1.5 to 18 days. Disturbed nests had at least one missing egg or one egg with tooth marks or cracks. In 2010 we calculated exposure days on the basis of either marks on the clay egg or depredation of the quail egg. This metric was strongly correlated with exposure days calculated on the basis of only depredation on the quail egg (Spearman $r = 0.85$, $p < 0.001$). We averaged exposure days for all nests at the same height in each plot for each year and used mixed-effects regression analyses to relate the dependent variable of mean exposure days per nest per plot to a suite of independent plot-level variables, including building density, mean temperature, slope, aspect, nest visibility, deciduous canopy, deciduous subcanopy, and evergreen shrub. We followed the protocol for model selection for nested data recommended by Zuur et al. (2009). This protocol determines the appropriate random structure first with a complete set of parameters for the fixed effects. We used year as a random effect. Once we determined the optimal structure of the random component, we evaluated the fixed effects in a backwards-selection process in which we used the Akaike information criterion (AIC) to assess model fit and parsimony. We used R (version 2.12) (R Development Core Team 2008) for model selection. We considered all models with a ΔAIC < 2 equally supported and examined the residuals for evidence of heteroscedasticity and unmodeled trends. See Spence-Bailey et al. (2010) for a similar application of this technique.

The techniques we used to measure predator composition and relative abundance (clay eggs, track plates, and motion-triggered cameras) yielded continuous data on predator activity (number of eggs attacked by certain predators, total predator detections) and presence or absence of particular predator species. Correlation analyses and *t* tests were used on the continuous data, whereas contingency-table analyses were used on predator-detection counts. We applied Fisher's exact tests to the count data because our sample sizes were small.

We sorted the clay eggs marked by predators into groups on the basis of photographs from the cameras and museum skulls of potential predators. We grouped predators into 1 of 5 categories: miscellaneous carnivore (including striped skunks, weasels, and domestic dogs and cats); Corvidae (American Crows and Blue Jays); opossums; raccoons; and Rodentia (including American red squirrels, eastern gray squirrels, eastern chipmunks, and deer mice [*Peromyscus* spp.]). We used a paired *t* test to determine whether the number of clay eggs depredated at each plot varied as a function of nest position (ground nests, $n = 36$; tree nests, $n = 36$) and correlation tests to determine whether the number of clay eggs depredated at each plot varied as a function of nest position, building density, and mean temperature. We used Fisher's exact tests to determine whether the presence or absence of each predator group at each plot, on the basis of depredation of clay eggs, varied as a function of nest position, building density (low, < 0.7 buildings/ha, $n = 20$ plots; high, >0.7 buildings/ha, $n = 16$ plots), and mean temperature (low, <20.7 °C, $n = 18$ plots; high, >20.7 °C, $n = 18$ plots). We did not correct *p* values for multiple comparisons (Moran 2003).

We used tracks from track plates and photographs to determine predator species presence and level of activity at each plot. All tracks left by the same mammal species on the 2 track plates at the same plot during the same sampling period were considered a single detection. Likewise, all photographs taken of the same mammal species at the same plot within 1 hour were considered a single detection. We examined whether predator presence varied as a function of building density and mean temperature. We calculated the total number of mammal detections during all 3 sampling periods for each plot and used correlation tests to determine whether the total detections varied as a function of building density and mean temperature.

Results

Of the 360 nests deployed each year, 207 (58%) were depredated by the end of the 18-day study in 2009 and 189 (53%) were depredated in 2010. Depredated quail eggs were either missing (84% in 2009, 81% in 2010) or shells were left inside or outside the nest. The model for average exposure days per nest with the lowest AIC included year as a random variable and mean temperature and nest height as fixed effects (Table 1). The average

Table 1. The 3 models of the relation among nest-exposure days (survival), temperature, and habitat variables that were most strongly supported by the data.

Model rank	*Independent fixed-effect variables*[*]	*Akaike information criterion (AIC)*	*ΔAIC*
1	− temperature + nest height	851	0
2	− temperature − buildings + nest height	854	3
3	− temperature − buildings + edge + nest height	867	16
Full model	− temperature + slope + insolation − buildings + visibility + canopy + subcanopy − shrub + nest height + predators	880	29

[*] *Year was included as a random effect in all models. Sign shows the direction of the effect on nest survival. Variable definitions: temperature, average daily mean temperature during the breeding season; slope, terrain slope in degrees; insolation, transformed aspect of slope with high values to southwest; buildings, buildings per hectare within 200 m of plot; visibility, percent visibility of nest from 3 m; canopy, subcanopy, shrub, factor scores measuring vertical distribution of vegetation in these layers; nest height, 0 (ground nest) or 1 (tree nest); predators, total number of predator detections at plot.*

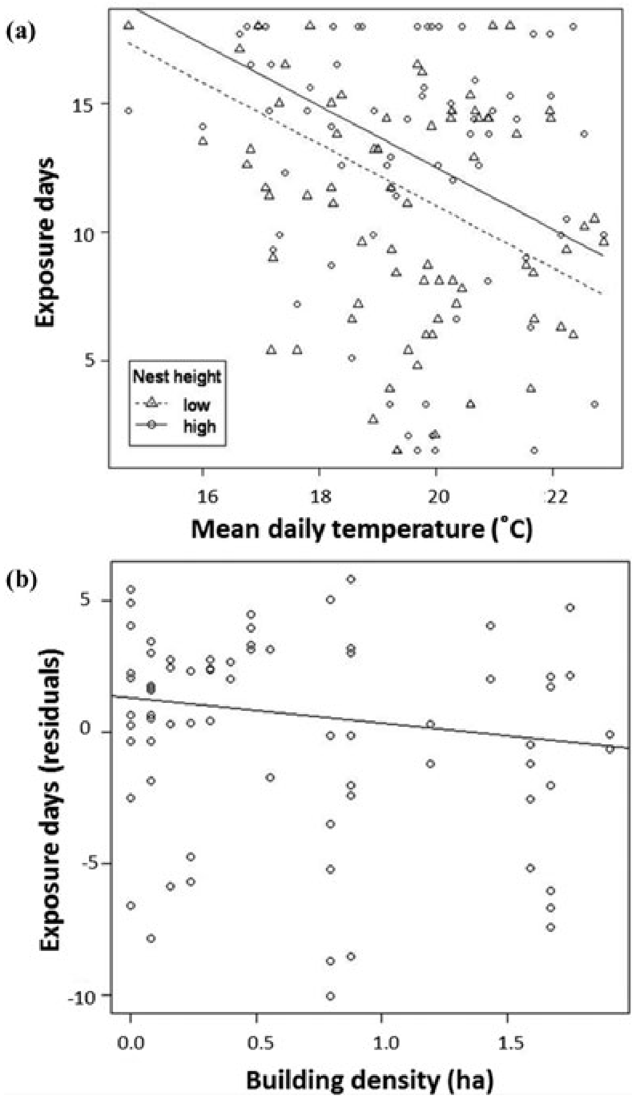

Figure 2. Nest survival as measured by exposure days (number of days during the 18-day nest-predation study until the nest was disturbed by predators) relative to temperature (°C), nest height, and housing density: (a) mean exposure days of 5 nests in 36 plots over 2 years (low, nests on the ground; high, nests >1.0 m aboveground; lines, trends estimated from regression analyses) and (b) residual variation in exposure days relative to building density (number of buildings per hectare) after correcting for effects of temperature and nest height (line, trends estimated from regression analyses).

number of exposure days per nest declined as mean temperature increased ($\beta = -1.2$ [SE 0.28], $p < 0.001$), and nests placed in trees had more exposure days than those on the ground ($\beta = 1.5$ [0.75], $p = 0.05$) (Fig. 2). The next best model (ΔAIC = 3) included year as a random effect and had fixed effects for mean temperature ($\beta = -1.1$ [0.28], $p < 0.001$), nest height ($\beta = 1.5$ [0.74], $p = 0.05$), and building density ($\beta = -0.1$ [0.05], $p = 0.07$).

The clay egg surveys yielded 125 clay eggs with identifiable predator imprints and 218 eggs that were undisturbed. Clay eggs in ground nests were depredated about twice as often as those placed in trees (average 2.3 versus 1.2 depredated nests/plot, respectively; $t = 3.87$, df = 35, $p < 0.001$). The total number of clay eggs depredated in each plot increased as building density increased ($r = 0.28$, $p = 0.10$), but did not vary as a function of mean temperature ($p = 0.31$). Clay eggs were most commonly depredated by rodents (45% of eggs, 75% of plots), less so by corvids (22% of eggs, 36% of plots), opossums (18% of eggs, 36% of plots), miscellaneous carnivores (8% of eggs, 22% of plots), and raccoons (7% of eggs, 19% of plots) (Fig. 3).

The types of predators detected with clay eggs varied as a function of nest position (Fig. 3a). Opossums and miscellaneous carnivores depredated more ground nests than tree nests. Corvids depredated tree nests more often than ground nests. For most groups of predators, detections of predators with clay eggs did not vary as a function of building density (Fig. 3b) or mean temperature (Fig. 3c); however, corvids were detected more often at high building density (Fig. 3b).

Track-plate surveys resulted in 164 detections of 12 species of mammalian predators (Table 2). The total number of detections in each plot did not vary with building density ($p = 0.28$); however, the total number of detections in each plot tended to increase as mean temperature increased ($r = 0.29$, df = 34, $p = 0.08$). More raccoon tracks were found on track plates (38% of detections) than any other species. Opossum, chipmunk, black bear, and domestic cat tracks were found less often (15%, 13%, 7%, and 7% of tracks, respectively). Domestic cat tracks appeared most frequently in plots with high building density (Fig. 4a) and warmer temperatures (Fig. 4b). The presence of other species did not vary as a function of building density or temperature.

Motion-triggered cameras took 104 photographs of 10 different species of mammalian predators (Table 2). White-tailed deer (*Odocoileus virginianus*), which have recently been documented as opportunistic nest predators (Pietz & Granfors 2000; Ellis-Felege et al. 2008), were detected most frequently.

Discussion

Nest survival declined as temperature increased and to a lesser degree as exurban development increased. These results indicate increased nest predation pressures may accompany climate change and exurban expansion in the southern Appalachian Mountains (Wear & Bolstad 1998; Mearns et al. 2003; Gragson & Bolstad 2006). We think

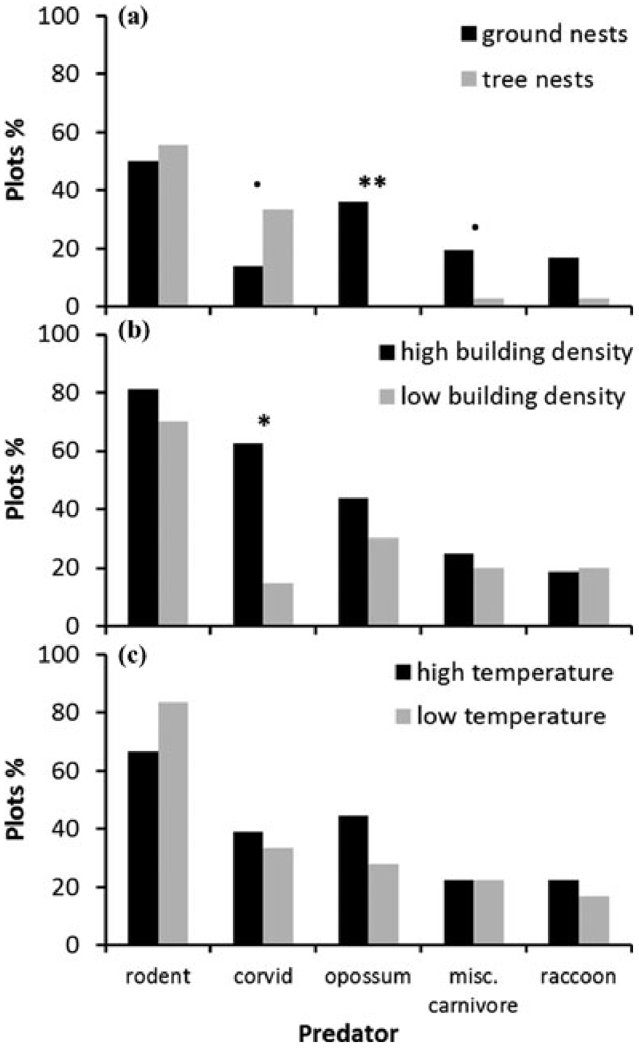

*Figure 3. Percentage of plots in which predators were detected with clay eggs at (a) ground and tree nests (*n *= 36 plots for both positions), (b) high and low building density (*n *= 18 for both densities), and (c) high and low mean temperature (*n *= 16 and 20 plots respectively). Significant differences (Fisher's exact tests):* $^{**}p < 0.001$, $^{*}p < 0.05$, $^{\bullet}p < 0.1$.

these environmental changes may pose a greater threat to ground-nesting birds than to tree-nesting birds because more nests on the ground were depredated than nests in trees. Only a few of the predator species we detected varied as a function of mean temperature or building density, but many of these predators are endothermic habitat generalists.

The mechanisms that contribute to declines in nest survival at higher temperatures are unclear because temperature and elevation were closely correlated and because our methods did not readily detect some nest predators whose presence is likely to vary as a function of mean temperature. In particular, we did not detect any reptiles even though black rat snakes and black racers (*Coluber constrictor*) occur in the region and are common nest predators (Thompson et al. 1999; Weatherhead et al. 2003; Weatherhead et al. 2010). Predation of quail eggs (Farnsworth & Simons 2000) and of nestlings (Williams & Wood 2002) by black rat snakes has been documented with video cameras. Our motion-triggered cameras may have been unable to detect snakes. Snake activity and abundance increases as temperature increases (Zamora-Camacho et al. 2010), and increases in activity may increase nest predation (Weatherhead et al. 2010). The increased nest predation at warmer temperatures that we found may have been partially due to predation by snakes.

Each degree of increase in mean temperature resulted in a little over 1 day of decline in average exposure days per nest. As temperature increases, cooler, high-elevation areas will have temperatures similar to current temperatures in low-elevation areas. An increase of 4 °C in mean temperature during the breeding season (half of the difference between our warmest and coolest plots) may decrease nest survival by an average of 4.8 days per nest. This increased risk of nest predation due to warming could be especially detrimental to species that have already declined as housing density increased (e.g., interior-forest specialists and Neotropical migrants) (Kluza et al. 2000).

Expanding exurban development may also increase the risk of nest predation. Domestic cat and corvid presence increased as building density increased. Exurban development can create edges that provide high-quality habitat for American Crows and Blue Jays, and snakes are often more abundant and active in edges (Chalfoun et al. 2002). Homeowners can reduce predation by domestic cats and dogs on nestlings, nesting adult females (Lepczyk et al. 2003; Baker et al. 2008; Balogh et al. 2011), and eggs (Lenth et al. 2008) by restricting outside movements of their pets.

Land-use planning can also mitigate the effects of expanding exurban development on nest predation. Clustering rural housing development minimizes the effect of houses on surrounding forest by overlapping the disturbance zone surrounding each house, decreasing edge, and increasing landscape connectivity (Theobald et al. 1997; Odell et al. 2003; Gagné & Fahrig 2010). Consideration of the ecological significance of the land that is developed may also mitigate the effects of expanding exurban development because the quality of remaining undeveloped lands may be more important to bird species than the quantity of undeveloped land (Freeman & Bell 2011).

Our results suggest that ground nests were at greatest predation risk from mesopredators (e.g., opossums, skunks, dogs, cats, and weasels). Nest survival was lower by an average of 1.5 exposure days for ground nests relative to tree nests—an effect larger than a 1 °C increase

Table 2. Summary of mammalian species detected with track plates (deployed in 36 plots) and motion-triggered cameras (deployed in 12 plots).

	Track plate		*Camera*
Species	*no. of plots*	*no. of detections*	*no. of detections*
Raccoon (*Procyon lotor*)	33	63	15
Opossum (*Didelphis virginiana*)	24	41	12
Chipmunk (*Tamias striatus*)	16	21	15
Black bear (*Ursus americanus*)	9	12	1
Domestic cat (*Felis catus*)	7	12	5
Red fox (*Vulpes vulpes*)	4	5	0
Domestic dog (*Canis lupus familiaris*)	4	4	1
Skunk (*Mephitis mephitis*)	2	2	0
Gray squirrel (*Sciurus carolinensis*)	1	1	16
Mouse (*Peromyscus* spp.)	1	1	7
Red squirrel (*Tamiasciurus hudsonicus*)	1	1	0
White-tailed deer (*Odocoileus virginianus*)	1	1	31
Coyote (*Canis latrans*)	0	0	1

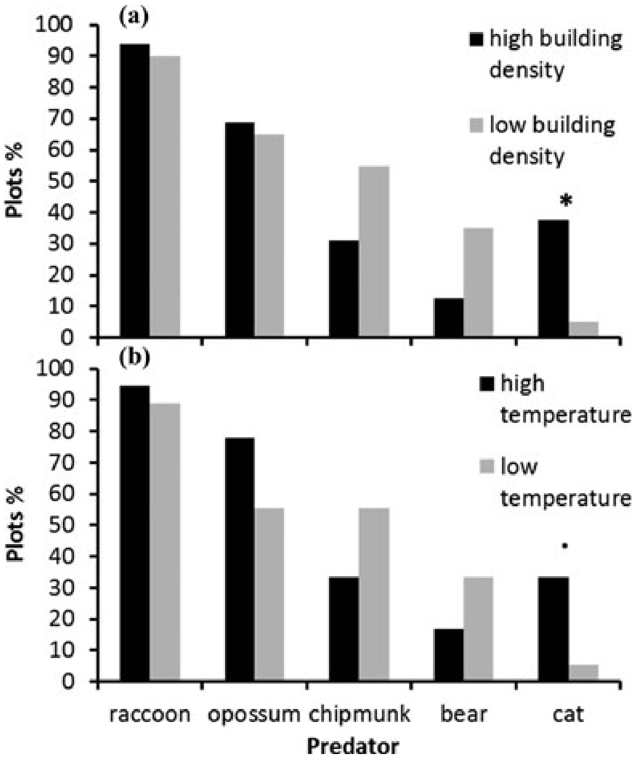

Figure 4. Percentage of plots in which predators were detected with track plates at (a) high and low building densities ($n = 16$ *and 20 plots, respectively) and (b) high and low mean temperature (*$n = 18$ *and 18 plots, respectively). Significant differences (Fisher's exact tests):* $^{**}p < 0.001$, $^{*}p < 0.05$, $^{\bullet}p < 0.1$.

in mean temperature. These results indicate that populations of ground-nesting birds at higher elevations, such as Canada Warbler (*Wilsonia canadensis*), Dark-eyed Junco (*Junco hyemalis*), and Veery (*C. fuscescens*), may be especially vulnerable to increased predation associated with increasing temperatures because they already experience greater predation relative to tree-nesting species.

Increased nest predation may result in unexpectedly large declines of regional populations of bird species if changes occur in source habitats (Porneluzi & Faaborg 1999; Hansen & Rotella 2002). For example, if continuous forests at high elevations act as a source for forest-interior and Neotropical migrant species, increases in temperature may increase risk of nest predation and reduce populations of breeding birds. Overall, our results suggest that increases in temperature will likely increase nest predation risk for birds in the southern Appalachian Mountains, especially forest-interior specialists and Neotropical migrants that nest on the ground, and exurban expansion may exacerbate these effects.

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