

## Predation rate on artificial nests increases with human housing density in suburban habitats

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Thorington, K. K. and Bowman, R. 2003. Predation rate on artificial nests increases with human housing density in suburban habitats. – *Ecography* 26: 188–196.

Predation causes most nest failure in birds. Predator communities are likely to vary across a gradient of increasing urbanization, so nest predation also is likely to vary across this gradient. Although predation is thought to decline with increasing urbanization, relatively little is known about variation in predation pressure within strata along an urban gradient and how factors known to affect nest success, such as nest location, interact with urban variables, such as human housing density. Native habitats are frequently fragmented and isolated by suburban residential development, thus we quantified predation rates on artificial nests located in natural oak scrub patches within a suburban matrix in south-central Florida. We examined patterns of predation based on nest location relative to habitat edges, artificial nest weathering treatment, nest shrub height, and human housing density. Over two 18-d trials, we placed a total of 240 nests, each containing a single quail egg and a clay sham, along three roadside transects. Nest predation was not influenced by proximity to edge, nest weathering, or trial date, but was highest at high housing density and lowest at low housing density. The proportion of quail eggs removed from nests increased with human housing density. Birds were the most frequent predators of artificial nests, but the relative frequency of predation by birds or mammals did not differ relative to any of our treatments. Higher rates of nest predation with increasing human housing density within suburban habitats may reflect changes in habitat structure and composition that increase the vulnerability of nests to predation or changes in the composition of the predator community. Our results modify the conclusions of previous studies by suggesting that at scales smaller than the entire urban gradient, nest predation may increase with human housing density, one common measure of urbanization.

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Throughout the world, human settlement has significantly transformed natural landscapes, and human populations are becoming increasingly urban (Marzluff 2001). Urbanization is “the anthropogenic conversion of natural ecosystems into human dominated ecosystems” (Gering and Blair 1999), thus by this definition the process of urbanization begins once natural habitats are altered by human settlement and includes a gradient of human settlement density from rural areas to higher density suburban and urban areas. Throughout this gradient, urbanization results in the loss, fragmenta-

tion, and perforation of natural habitats (Miller et al. 2001) and in the concordant changes in the structure and composition of floral (Reichard et al. 2001) and faunal (Mackin-Rogalska et al. 1988, McIntyre 2000) communities.

Avian community structure and composition vary with urbanization (Aldrich and Coffin 1980, Beissinger and Osborne 1982, Mills et al. 1989, Jokimäki and Suhonen 1993). Urban bird communities often are more dense, but less diverse and less rich because they tend to be dominated by one or a few synanthropic

Accepted 20 June 2002

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ISSN 0906-7590

species (Johnston 2001). However, to understand how avian communities change with urbanization it is necessary to examine the underlying variation in demographic patterns. Nest predation causes most reproductive failure in birds (Ricklefs 1969, Hatchwell et al. 1999, Buler and Hamilton 2000, Knutson et al. 2000) and has thus become a focus of many studies examining the impacts of habitat alterations on avian demography, especially that of habitat fragmentation and edge effects (for reviews see Paton 1994 and Chalfoun et al. 2002). Predator communities may differ between natural and urbanizing habitats, but relative patterns of increasing and decreasing predator abundance may be scale-dependent. In general, predators may decline in abundance near the urban end of the gradient (Wilcove 1985, Donovan et al. 1997), but this may vary by landscape and predator type. Within suburban habitats, the abundance of generalist predators, both avian and mammalian, may increase with increasing human housing density (Jokimäki and Huhta 2000, Haskell et al. 2001). Predator-prey interactions are often scale-dependent (Schmidt et al. 2001); the landscape within and surrounding individual sites along urban gradients is likely to vary and influence predation pressure within and among sites across the entire urban gradient (Clergeau et al. 1998, 2001, Gering and Blair 1999).

In recent years, artificial nest studies have been used to examine the effects of habitat alterations on avian nest success. The value in this method lies in making relative comparisons among treatments rather than absolute estimates of rates of nest predation (Part and Wretenberg 2001, Zanette 2002). Previous urban studies have compared predation rates on real or artificial nests between sites, such as rural and urban areas (Tatner 1982, Eden 1985), or across a gradient of urbanization (Gering and Blair 1999, Kosinski 2001) and virtually all have concluded that nest predation declines with increasing urbanization (but see Melampy et al. 1999, Jokimäki and Huhta 2000). Although many artificial nest studies in natural habitats evaluate the effect of variables that are known to affect nest success, relatively few studies in urban landscapes have done so.

Nest site may affect the risk of predation (Davison and Bollinger 2000). If urban landscapes are heterogeneous at multiple scales, selection of nests sites also is likely to vary across and within sites along an urban gradient. Landscape variation at the "backyard" scale may lead to variation in the amount and context of habitat edges within a site. The negative effects of edge on avian nest survival in forest patches and fragmented landscapes are well documented (Paton 1994, Hartley and Hunter 1998, Willson et al. 2001; but see Lahti 2001); however, the extent of edge effects and how far they penetrate a habitat patch is not well known and may be species and landscape dependent (Paton 1994, Donovan et al. 1997, Lahti 2001).

Artificial nest studies provide good models to explore the questions of urbanization and edge effects on nest predation and offer several advantages over studies of natural nests (Major and Kendal 1996). Nest location and specific treatment effects can be controlled and sample sizes can be relatively large. Predation is relatively easy to discern and the identity of predators often can be inferred from imprints in sham eggs. Artificial nest studies also have limitations (see review Major and Kendal 1996). Many studies have attempted to overcome these limitations by trying to make experimental nests similar to real birds' nests, such as weathering nests before they are placed in the field, but rarely are the results of these efforts evaluated.

We sought to document variation in predation pressure within a suburban habitat and assess possible sources of this variation by examining factors that are known to influence nest success. Our objectives were to determine if predation rates on artificial nests differ 1) across a gradient of human housing density within a suburban subdivision; 2) between nests at the edge or interior of habitat patches within the suburban matrix; 3) between nests with different color and weathering treatments; and 4) to determine the major egg predators and how they vary relative to housing density, edge, and time of season.

## Study site and methods

### Study site

This study was conducted during spring 2001, in Placid Lakes Estates (PLE) (27°15'N, 81°25'W), a residential subdivision 5 km southwest of Lake Placid, in south-central Florida. The native habitat patches in PLE consist primarily of xeric oak *Quercus* spp. scrub, rosemary *Ceratiola ericoides* scrub, sand pine *Pinus clausa* scrub, scrubby flatwoods (Myers and Ewel 1991) and a variety of human-disturbed habitats. A long-term study of the effects of urbanization on Florida scrub-jays *Aphelocoma coerulescens* at this same site has been ongoing since 1993 and was concurrent with the present study. See Bowman and Woolfenden (2001) for a more detailed description of the study area.

### Methods

Within PLE natural habitats occur as patches within a matrix of human settlement, where house density ranges from < 20 houses/40 ha to > 180 houses/40 ha. At the low end of the range in housing density, relatively large tracts of scrub are fragmented by roads and perforated by single-family residential development. At high housing density, small scrub patches exist surrounded by roads and dense human development. As

part of a larger study (Bowman and Woolfenden 2001), we mapped each house and used the GIS procedure KRIG in Arc/Info (Mitchell 1999) to construct a contour map of housing density based on isocline intervals of 20 houses/40 ha. Because only a relatively small proportion of our study site had housing densities exceeding 40 houses/40 ha, we pooled all density classes above that density into a single, high density class. Thus, for analytical purposes, we defined three housing-density classes: low density (<20 houses/40 ha), medium density (20–40 houses/40 ha), and high density (>40 houses/40 ha). We placed 40 artificial nests along each of three transects, each located within one of the three housing density classes. Within a transect the housing density surrounding nests varied within the limits of each housing-density class. Thus, we also counted the number of houses within a 10 ha circle centered on each nest. We chose this area to minimize overlap between adjacent nests and thus reduce spatial autocorrelation. Transects were not linear, but followed secondary roads.

We used commercially available bamboo canary nest baskets, ca 10 cm in diameter and 6 cm deep. We attached the nests to trees and shrubs with brown postal twine. All nests were placed between 1 and 2 m above ground, depending on the best possible location to tie the nest. We measured the height of the shrub in which the nest was placed to the nearest 0.1 m.

In addition to housing density and nest-shrub height, we had two experimental treatments: proximity to habitat edge and nest weathering. The four possible treatment combinations for each nest were: light colored, minimally weathered nests near a habitat edge (LE), light nests away from habitat edges (LI), dark colored, more extensively weathered nests near edges (DE), and dark nests away from edges (DI). Nests were weathered but otherwise not modified to resemble the nests of any particular species of bird. Nest color was partially determined by the amount of nest weathering. Light nests were new and weathered outdoors for about a week prior to the experiments. Dark nests had been dyed brown and were extensively weathered. We placed edge nests within 3 m of a habitat edge and interior nests at least 10 m from an edge. Nests within 3 m of the edge were usually easily visible from the edge whereas interior nests were not. We defined an edge as the start of unmowed vegetation along the road. Because the road included a shoulder of mowed grass, edge nests tended to be 4–6 m from the actual road surface. All edges were along roads, as opposed to backyards or other edge types; however, in a few cases these edge types could not be avoided. Nests were placed every 25 m in native habitat patches, excluding yards and posted property. If a placement point was unsuitable we continued along the transect until the next suitable location, thus in some instances adjacent nests may have been >25 m apart, but nests were

never closer than 25 m. Treatments were alternately assigned to sequential nests along a transect.

We conducted two trials to assess the effects of time period on predation rates. In many passerines, including the Florida scrub-jay, a relatively common passerine within our study area, nest success declines through the breeding season (Woolfenden and Fitzpatrick 1996). We conducted the first trial from 10 April to 1 May and the second from 15 May to 4 June: the exposure period for all nests was 18 d. Nests were visited every 6 d over the 18 d period for each of the two trials. Each transect consisted of 40 nests for a total of 120 nests/trial and an experiment total of 240 nests.

At the beginning of each trial, we placed two eggs in each nest, one coturnix quail *Coturnix japonica* egg and one clay sham egg. Quail eggs were kept refrigerated until placed in nests. DeGraaf et al. (1999) concluded that the use of large eggs, such as coturnix quail eggs, in artificial nest studies could bias results because predators with small gapes cannot bite large eggs. We added one clay sham egg, ca 25% smaller than the quail egg, to each nest to minimize the potential bias against small predators. Sham eggs were made with a modeling compound, and hand-shaped to resemble real eggs. Shams were tethered to the nest basket (Major et al. 1996) to prevent predators from removing them. Shams were smoothed again after they were tethered.

During each 6 d visit we inspected each nest for evidence of predation. Depredated nests were removed at that visit, but surviving nests were removed only at the end of the trial. Nests were considered depredated if either egg or sham were missing or if either egg or sham had a hole in it or scratch on it. We collected any egg fragments found outside the nest for predator analysis. Each egg or sham that was preyed upon was examined in the lab and assigned to one of four predator categories: bird, mammal, both bird and mammal on the same egg, and unknown.

We used photographs from Major (1991) and Sowls (1948) to identify predators associated with different imprints left in shams and marks on quail eggs. Eggs preyed upon by small mammals show bites and scratches, often concentrated near but not restricted to the ends of the egg. Shams that have been attacked by mammals often contain deep incisor marks and could be so damaged that only small bits of masticated clay remain in the nest. Larger mammals leave larger tooth imprints and are likely to cause more physical disturbance at nests (Langen et al. 1991, Jobin and Picman 1997). Mammals create relatively large holes in eggs and often leave the amniotic membrane curling into the egg; holes made by birds tend not to have this characteristic (Sowls 1948). Bird predation consists of holes pecked in eggs and foot and bill marks on shams. Bird predation can be inferred when eggs have one large hole in the side (Jobin and Picman 1997). Bird predation also can be inferred from small dents and holes

without apparent scratching or scraping. Bill marks in clay appear as triangular wedges removed from the sham or many deep holes and shallow peck marks in the clay. Tethered clay shams are sometimes pulled like taffy or are covered in long circular scratches caused by being grasped in a bird's beak or foot. Bird footprints on clay shams often look like exclamation marks- the dash formed by the fleshy part of each toe with the hole formed by each claw. We presented several sham and real eggs to Florida scrub-jays to familiarize ourselves with imprints made by birds on both types of eggs.

As part of the ongoing demographic research on Florida scrub-jays, all territories of this corvid had been mapped within the study area. Because jays themselves may be potential predators of passerine nests and the data were available on the distribution of jays within the study area, we also tested if experimental nests within scrub-jay territories were depredated more frequently than nests outside of jay territories.

### Data analysis

We compared nest survival rates between housing density transects, edge and weathering treatments, trials, nest-shrub height, and whether a nest was adjacent to or within a territory of Florida scrub-jays. We tested all data for normality and homoscedascity. We opted not to use the frequently employed Mayfield method for testing differences in nest success, because this method corrects for a bias that did not exist in our database. We used a  $\chi^2$  test to test for differences in the frequency of nest predation between classified variables (edge, weathering, housing density class, proximity to scrub-jay territories, and trials). For nest-shrub height, a continuous variable not normally distributed, we used a Mann-Whitney U-test to test for differences between depredated and successful nests. To test the effect of variation in housing density within transects, we used logistic regression (Norušis 1999) to test the relative effects and interactions between all categorical treat-

ments, nest-shrub height, and housing density measured as a continuous variable at each nest site. Housing density measured at each nest was spatially autocorrelated (Mantel test,  $p < 0.05$ ). To achieve statistical independence, we randomly removed one nest from each pair of adjacent nests, thereby eliminated overlap, and used this subset in the subsequent analysis. We used Kaplan–Meier survival analysis and the Breslow test for equality of survival distributions (Anon. 1999) to test for differences in the timing of nest predation among housing density classes. This method is useful for comparing differences in the time of occurrence of a critical event, in this case nest predation, among treatments.

We tested the repeatability of our subjective predator assignments. We took 50 eggs or shams, 10 each for those preyed upon by bird, mammal, both bird and mammal, or unknown, and 10 unmarked eggs and asked seven independent observers to assign eggs as either depredated or not, and if depredated, by which of the four predator assignments. To test the similarity of our predator classification among seven independent observers we calculated the percentage of eggs each observer classified similarly to our classification, arcsine transformed those values (Zar 1997), and then used one-way ANOVA to determine if those percentages differed among predator classes.

### Results

Nest survival was not influenced by proximity to edge or nest weathering ( $\chi^2 = 0.04$ ,  $DF = 1$ ,  $p = 0.84$ ;  $\chi^2 = 0.37$ ,  $DF = 1$ ,  $p = 0.54$ , respectively) (Table 1). Season did not influence nest survival; nest predation rates were similar between the two trials ( $\chi^2 = 0.04$ ,  $DF = 1$ ,  $p = 0.84$ ). Neither the height of the nest shrub nor proximity to a scrub-jay territory influenced nest survival (Mann-Whitney  $U = 2587.5$ ,  $p = 0.40$ ;  $\chi^2 = 0.38$ ,  $DF = 1$ ,  $p = 0.54$ , respectively). Nest survival did differ significantly among the three transects ( $\chi^2 = 13.0$ ,

Table 1. Survival rates of artificial nests assigned to different treatments within a suburban residential development across a gradient of increasing human-housing density. Survival rates determined as the percentage of nests in which both sham and quail eggs were intact after the 18-d observation period (10 nests/treatment, 40 nests/transect, 120 nests/trial [Trial 1, 10 April–1 May; Trial 2, 15 May–4 June] and 240 nests for the entire experiment). Treatment designations are LI, lightly weathered/interior; LE, lightly weathered/edge; DI, darkly weathered/interior; DE, darkly weathered/edge.

Housing density	Trial	LI	LE	DI	DE	All nests
Low	1	0.20	0.10	0.30	0.20	0.20
Medium	1	0.10	0.00	0.10	0.10	0.08
High	1	0.00	0.10	0.00	0.10	0.05
Trial total	1	0.10	0.07	0.13	0.10	0.11
Low	2	0.10	0.30	0.20	0.30	0.23
Medium	2	0.20	0.10	0.10	0.00	0.10
High	2	0.00	0.00	0.00	0.10	0.03
Trial total	2	0.10	0.13	0.10	0.13	0.12
Total both trials	–	0.10	0.10	0.12	0.12	0.11

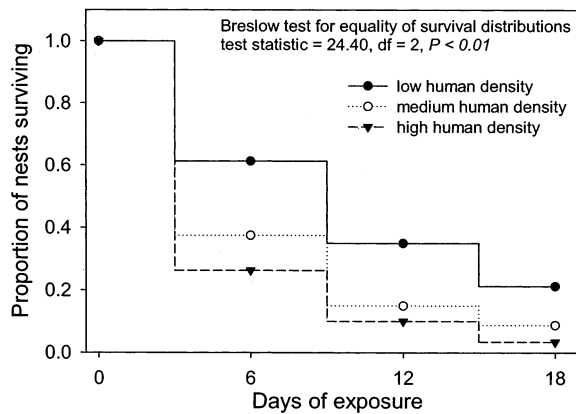


Fig. 1. Daily nest survival probabilities of experimental nests based on a Kaplan–Meier survival analysis of nests within a suburban residential development across a gradient of human-housing density.

DF = 2,  $p = 0.002$ ), reflecting a difference in nest survival relative to human housing density. Survival distributions were significantly different among the three transects (Breslow test statistic = 24.4,  $p < 0.01$ ); more nests were depredated during the first 6 d interval at medium and high housing density than at low housing density (Fig. 1). Only human housing density was retained in the logistic regression model as a significant predictor of nest survival (Table 2).

Of the 240 quail eggs used in both trials, 142 (59.2%) were removed from nests. Despite being tethered, 12 of 240 (5%) sham eggs were removed. At 11 nests, we found no eggs remaining in the nest, but egg remains were collected from underneath five of these nests. We found a significant difference in the proportions of quail eggs removed from nests between the three transects ( $\chi^2 = 7.2$ , DF = 2,  $p = 0.03$ ). The proportion of quail eggs removed increased with human housing density (48%, low density; 63%, medium density; 68%, high density).

On several occasions we observed Florida scrub-jays or blue jays *Cyanocitta cristata* taking quail eggs or pulling on clay shams from experimental nests. Rodent fecal matter also was found in several nests. Most of

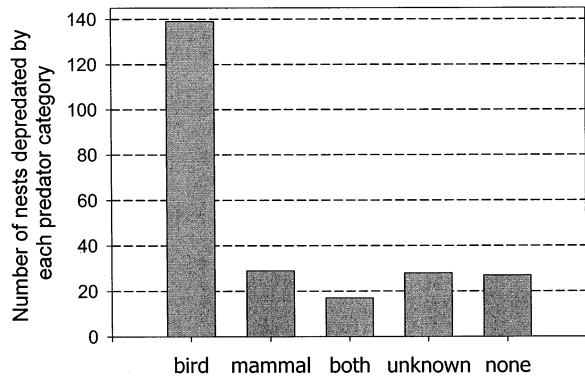


Fig. 2. Frequency of predators identified from markings on quail eggs and clay shams at depredated experimental nests in oak scrub patches imbedded in a suburban matrix in south-central Florida ( $\chi^2 = 185.78$ , DF = 3,  $p < 0.001$ ).

the predators identified from markings on clay shams were birds (58%); birds were scored as the nest predator significantly more frequently than mammals, both birds and mammals, and unknown predators ( $\chi^2 = 185.78$ , DF = 3,  $p < 0.001$ , Fig. 2) and more frequently than all other predators combined. This pattern also existed when compared between individual treatments or for other independent variables. We found no significant differences in the proportion of nests scored as being preyed upon by the different predator classes between trials ( $\chi^2 = 4.75$ , DF = 1,  $p = 0.19$ ), by the day of nest failure (day 6, 12, or 18) ( $\chi^2 = 7.90$ , DF = 2,  $p = 0.25$ ), between edge and interior nests ( $\chi^2 = 2.79$ , DF = 1,  $p = 0.43$ ), between dark and light nests ( $\chi^2 = 0.86$ , DF = 1,  $p = 0.83$ ) or between transects ( $\chi^2 = 2.75$ , DF = 2,  $p = 0.84$ ).

Our method of scoring depredated eggs into different classes of predators was relatively repeatable. The ability of independent observers to score eggs in the same manner that we scored eggs differed by predator class ( $F_{1,6} = 30.67$ ,  $p < 0.001$ ). Independent observers frequently scored unmarked eggs and eggs preyed upon by birds or mammals in the same manner as we scored the eggs. However, eggs scored as preyed upon by both birds and mammals and those preyed upon by unknown predators were less frequently scored similarly

Table 2. Variables selected by stepwise backward conditional logistic regression as predictors of nest predation of experimental nests across a human density gradient. Variables not in the equation are listed in the order that were removed from the model.

Variable	$\beta$	SE	Wald Statistic	DF	$p$
Variables in the equation					
Housing density	0.017	0.006	7.103	1	0.008
Constant	1.346	0.292	21.00	1	<0.001
Variables not in the equation					
Shrub height	0.018	0.204	0.008	1	0.920
Trial	0.084	0.417	0.041	1	0.840
Edge	-0.090	0.417	0.047	1	0.820
Proximity to jays	-0.124	0.418	0.088	1	0.760
Weathering	0.265	0.418	0.402	1	0.520

by ourselves and the seven observers. In the field, most eggs scored as unknown were missing from the nest, but in our scoring test, most of these eggs were ambiguously marked, thus observers often assigned them to one of the other predator classes. Eggs scored as preyed upon by both birds and mammals were usually scored by independent observers as either bird or mammal, but not both, suggesting that once a predator was identified, the observers stopped examining the eggs.

## Discussion

We have shown that within suburbs predation of artificial nests in patches of natural habitats increases with human housing density, but was not affected by proximity to habitat edges or territories of a potential avian predator, by nest-shrub height, by season or by weathering to make artificial nests more like real birds' nests. Our results differ from other studies, in that we demonstrate variation in predation pressure on artificial nests at one stratum within the larger continuum of the urban gradient and demonstrate a potential source for that variation.

Gering and Blair (1999) reported an increase in the survival rates of artificial nests across a gradient of increasing urbanization; we observed the opposite pattern. However, the scale of the urban gradient differed between these two studies. Gering and Blair's (1999) study ranged from wildland preserves to industrial parks; ours occurred within a suburban area, but across a gradient of increasing human housing density. Within towns in Finland, nest predation was higher in the town center than in an area of lower human density detached housing (Jokimäki and Huhta 2000). Predator species may be quite different in habitats at extreme ends of the urban gradient, but subtler differences may exist in the structure of the predator community at adjacent levels of the urban gradient (Wilcove 1985, Melampy et al. 1999). Beside scale, landscape context also could influence predation rates. Nest predation rates are higher in smaller woodlots than in larger ones and higher in habitat patches surrounded by suburban development than in those surrounded by agriculture or continuous woodlands (Wilcove 1985). Melampy et al. (1999) found no significant differences between predation rates in rural and suburban woodlots, but in their study rural woodlots were surrounded by "more extensive cropland" that might provide food for some mammalian nest predators, thereby increasing the predation pressure in the more rural setting. The differences among these studies suggest the importance of scale and landscape context in assessing the potential risk of predation. Several studies have suggested that the relationships between habitat edges, predator abundance and nest predation may be both scale and land-

scape-specific (Dijak and Thompson 2000, Lahti 2001, DeSanto and Willson 2001).

We did not detect any effect of habitat edge on nest predation, but most of our interior nests were within 10–15 m of the habitat edge. The deleterious effect of edges often extends 30–50 m or more into adjacent habitat patches (Brand and George 2000, Winter et al. 2000). In our suburban area, nests located farther than 15 m from one edge often were within this distance to an edge on the opposite side of the patch. At this scale of patch size and habitat fragmentation, virtually all habitat patches available to nesting passerines are likely to be influenced by an edge. In part, this could explain the very high rates of nest predation we observed. Adequately testing an edge effect in suburban habitat would require variation in patch size greater than that available in our study area. However, in many suburban habitats, natural habitat patches are likely to be small and most birds are likely to nest within 10–15 m of an edge.

Predation rates on artificial nests have been used to infer predation on natural passerine nests, but increasing doubt exists if such comparisons are viable (Wilson et al. 1998, Butler and Rotella 2000, Davison and Bollinger 2000, Weidinger 2001). Artificial nests and their contents differ from real nests and eggs in ways that may alter their vulnerability to predation (Haskell 1995, Maier and DeGraaf 2000, Rangen et al. 2000). Artificial nests are not attended by birds (Cresswell 1997), but are frequently visited by researchers who may leave olfactory cues (Whelan et al. 1994, Skagen et al. 1999). Nest sites may differ from those selected by birds (Yahner and Piergallini 1998). Artificial nest densities are often higher than natural nest densities, and experimental nests often are more regularly dispersed than natural nests, which may allow trap lining by predators (Willebrand and Marcström 1988, Bayne and Hobson 1997, DeGraaf et al. 1999, Rangen et al. 2000, Willson et al. 2001). Methods have been developed to minimize the potential biases of using artificial nests. These methods include weathering (Rangen et al. 2000), adding natural materials to artificial nests (Wilcove 1985), and rigorous attempts to reduce human odors associated with artificial nests (Bergan et al. 1997, Donovan et al. 1997, Lewis and Montevecchi 1999, DeGraaf et al. 1999, Knutson et al. 2000, Rangen et al. 2000, 2001). In our study, weathering nests did not affect predation risk. We did not attempt to mask human odors, in part, because within small patches of habitat in a suburban matrix, human odors are likely to be ubiquitous. Human odor can increase predation rates by some terrestrial mammals, such as raccoons *Procyon lotor* (Whelan et al. 1994) but, in our study, most artificial nests were preyed upon by birds rather than mammals. For comparisons of predation rates between and within studies, uniformity of methods is probably more important for interpreting results than

are the specific methods used to make artificial nests resemble real nests.

Bird predation was more frequent than predation by mammals, but this pattern did not vary with human density. In Finland, most artificial nests in urban areas were preyed upon by birds (Jokimäki and Huhta 2000). This may reflect the composition of the local predator community or differences in the vulnerability of artificial nests to different predators. We did not attempt to quantify the relative abundance of different predators, but some potential avian and mammalian predators increase in abundance with human density (Haskell et al. 2001, Fleischer and Bowman unpubl.). Our methods are likely to exclude detection of some predators known to prey on birds' eggs. Snakes are likely to remove eggs and unlikely to bite clay shams. We found that the removal of quail eggs increased with human density, suggesting that snake predation also might increase with human density. Other nest predators may eat eggs and avoid shams and they too would be underrepresented based on our inspection of eggs and shams remaining in nests. Most mammalian predation was by small rodents, rather than the larger, terrestrial predators often associated with urban environments, such as raccoons, or opossums *Didelphis virginiana*. However, the effects of such predators would be reflected in the overall rate of nest predation.

In a previous study at the same site Bowman and Woolfenden (2001) found that predation of Florida scrub-jay nests did not vary across the same human housing gradient, in contrast to our results on artificial nests. These differing patterns might be consistent with predators in suburban habitats that increase in abundance with human density, but that are deterred from preying on the nests of Florida scrub-jays. Birds were the most frequent predator of artificial nests and many of the potential avian predators are fairly common in suburban habitats. In Finland, predation of artificial nests reflected the distribution of avian nest predators (Jokimäki and Huhta 2000). In some areas of the USA, blue jays, American crows *Corvus brachyrhynchos*, and common grackles *Quiscalus quiscula*, are more common along forest edges and in the suburban matrix than in contiguous woodlots (Wilcove 1985). In our study area, blue jays, common grackles, and northern mockingbirds *Mimus polyglottis* all increased in relative abundance with human density (Sewell and Bowman unpubl.). Florida scrub-jays could easily deter any of these species from preying on their nests, but these species may readily prey on unattended and undefended artificial nests. In addition, Florida scrub-jays themselves likely were predators of artificial nests, but unlikely to prey on the nests of other scrub-jays because of their highly territorial social system (Woolfenden and Fitzpatrick 1996).

Our results suggest that in suburban developments with existing patches of native habitat, predation rates

on artificial nests are relatively high and increase with human housing density. Although other studies have suggested that nest predation may decline with increasing urbanization (Miller 1998, Gering and Blair 1999), this pattern may vary within and between strata in the urban gradient. The gradient approach to understanding urban ecology is useful, but its application should not be restricted to the broadest landscape scales; it can and should be used within strata along the entire urban gradient. As suggested by the contrast in results between predation rates on artificial nests and on Florida scrub-jay nests (Bowman and Woolfenden 2001) within the same study area, predation patterns also may be species-specific. Suburban habitats may provide ideal habitats in which potential nest predators thrive. The combination of patches of native habitats and abundant sources of anthropogenic foods may increase the relative abundance of many types of potential predators, from snakes and birds, to rodents and larger terrestrial mammals. Although absolute rates of nest predation derived from studies of artificial nests should not be extrapolated to real nests, increases in nest predation rates as suburban areas become increasingly developed could alter the population dynamics for many bird species, turning population sources into sinks.

*Acknowledgements* – We thank Liza Merly, Craig Carter, and Arthur Fleischer for assistance in the field. We thank Kyle Ashton, Kim Brand, Craig Carter, Arthur Fleischer, Tina Fleischer, and Matthew Shawkey for assistance in testing our predator scoring system. Previous versions of the manuscript were improved by comments from Torgrim Breiehagen, Esteban Fernandez-Juricic, Arthur Fleischer, Jon Gering, Jack Hailman, Richard W. Thorington Jr, Walter Koenig and Glen Woolfenden. KT was supported by an undergraduate internship by Archbold Biological Station. Research in our suburban study area was supported by Archbold Biological Station and by NSF grant IBN-00777469 to RB.

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