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Do Urban American Crows (*Corvus brachyrhynchos*) Contribute to Population Declines of the Common Nighthawk (*Chordeiles minor*)?

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ABSTRACT.—Ground-nesting Common Nighthawks (*Chordeiles minor*), adapted to living and reproducing in North American cities, nest on flat-topped gravel roofs. But populations of Common Nighthawks have declined in recent years throughout their range. One hypothesis to explain these declines is that American Crows (*Corvus brachyrhynchos*), which have increased dramatically in

numbers in urban areas in recent years, may be depredating nighthawk nests. If urban crows are a factor in nighthawk declines, we predicted there would be higher rates of predation on nests in urban areas than in rural areas. We tested this hypothesis by placing and monitoring artificial nests containing *Coturnix* quail eggs in both urban and rural settings. Depredation of experimental clutches was significantly lower in rural, natural habitats than in the urban environment. The type of substrate on urban roofs may also be important in influencing rates of depredation, as egg-loss was more common at experimental nests on roofs with a small pea gravel substrate than on roofs covered in larger river stone. In all cases, identified predators were American Crows. While experimental predation rates may not

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represent actual levels of predation on natural nests, these relative differences in rates of predation suggest that urban crows may be an important contributor to declining populations of Common Nighthawks. Received 5 December 2014. Accepted 25 December 2015.

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Population declines of migratory avian aerial insectivores are increasing (Böhning-Gaese et al. 1993, Nebel et al. 2010, Sauer et al. 2014). The causes of these declines remain elusive, in part due to the diversity in life history and ecology among aerial insectivores (Nebel et al. 2010). However, Nebel et al. (2010) used North American Breeding Bird Survey (BBS) trend data to show that declines of aerial insectivores occur over a geographical gradient with more pronounced declines in northeastern North America. They concluded that the taxonomic breadth of the population declines implicates declines in populations of flying insects as a likely factor, and that insect declines are likely associated with the long-range transport of atmospheric pollutants associated with acid precipitation. But continental effects of the El Niño Southern Oscillation (Sillett et al. 2000, Wolfe and Ralph 2009), the North Atlantic Oscillation (Stokke et al. 2005), or climate-change related effects on insect abundance (Visser et al. 2006) and phenological mismatches (Both et al. 2006) could also produce geographical patterns in population trends (Nebel et al. 2010).

The Common Nighthawk (*Chordeiles minor*) is a long-distance migratory, aerial insectivore whose breeding range is widely distributed across North America. Population declines of this species have been detected through the BBS (Sauer et al. 2014), and a number of “second-generation” breeding bird atlases report declines of 52–78% over populations counted in first-generation atlases a decade or so earlier (summarized by Musher 2013). While hypotheses to explain declining population trends for the Common Nighthawk have included the ecosystem changes associated with the decline of aerial insects that make up their diet, the Common Nighthawk’s adaptability to anthropogenic habitats has focused attention on attributes of its nesting ecology to explain the declining numbers. The Common Nighthawk is a ground nester adapted to nesting on flat-topped gravel roofs

(Armstrong 1965, Poulin et al. 1996), especially in urban areas where warehouses and similar structures provide expansive nesting substrate. However, more recent changes in roof substrates, including the use of larger gravel, rubber, and other synthetic materials may result in the loss of optimal nesting substrates, decreased camouflage, or over-heating of eggs (Brigham 1989, Poulin et al. 1996, Musher 2013).

A non-mutually exclusive hypothesis to explain Common Nighthawk declines is that American Crows (*Corvus brachyrhynchos*), whose population has increased sharply in recent decades (Sauer et al. 2014), especially in urban areas (Marzluff et al. 2001), may be depredating rooftop nests frequently enough to contribute significantly to nighthawk declines. American Crow populations tend to be densest and increasing most rapidly in urban areas of North America (Marzluff et al. 2001). While many cities report increasingly large winter roosts of American Crows (Marzluff et al. 1994), Marzluff et al. (2001) suggest that urban crow numbers are driven by dispersal from breeding populations in suburban or rural areas where reproductive success is higher, and that dispersal of pre-breeding individuals to the city has been successful because of the ready availability of food. Crows appear adept at exploiting anthropogenic food resources, but whether or not they also consume considerable numbers of eggs and young of other birds is debated (Marzluff et al. 2001, Verbeek and Caffrey 2002). Marzluff et al. (2001) found that crows rarely preyed on artificial nests, but many other studies have shown a positive correlation between various indices of crow abundance and predation rates on nests (Angelstam 1986, Johnson et al. 1989, Andrén 1992). Whether crow predation might also include nests of Common Nighthawks has not been studied, although Musher (2013) conducted a preliminary study of predation at mock nighthawk nests using quail eggs and found that in Pittsburgh, PA there was “almost immediate” predation by American Crows. However, his sample size was small and there was no comparison made with predation rates at natural nest sites.

Here, we test the hypothesis that American Crows contribute to Common Nighthawk declines through higher rates of depredation on urban rooftop nests than nests in rural, natural habitats. We test this hypothesis using mock nests deployed on two types of gravel rooftops, and

compare our results with mock nests in mixed-grass prairie. While experimental predation rates may not represent actual levels of predation on natural nests, we expect that relative differences in rates of predation can inform a better understanding of declines of Common Nighthawks.

METHODS

Our experiment was carried out from June 27 – August 7, 2013 on the campus of the University of Wyoming, Laramie, Wyoming (41.313 N, 105.581W), and at the Spring Creek Preserve northwest of Laramie (41.795 N, 105.827 W). With a resident population of ~31,000 people (excluding most of the 13,000 students at the university), the urban and dense-residential area of Laramie covers ~45 km². Crows are abundant in the city (SCL, pers. obs.), but no population estimates are available.

Spring Creek Preserve is located at 2,195 m elevation near Rock River, Wyoming approximately 65 km northwest of Laramie. The undeveloped preserve is in the Laramie Basin and consists of ~2,600 ha of relatively pristine mixed-grass prairie which is seasonally grazed by ~120 head of cattle. The site is typical of natural nesting habitat for the Common Nighthawk with grasses and other prairie plants interspersed with bare ground, sand, lichen, and cobble where nighthawks tend to lay their eggs (Poulin et al. 1996). Common Nighthawks frequently nest on the site and American Crows are recorded as “common” (L. Musher and S. C. Latta, unpubl. data) and expected to be seen daily.

Because nighthawks lay their eggs on the ground without any structure being built, no imitation nests were required for our study. At locations consistent with nest sites described by Poulin et al. (1996), we placed two *Coturnix* quail eggs (Lake Cumberland Game Bird Farm and Hatchery, Monticello, KY, USA) together on the ground. *Coturnix* quail eggs measured ~3.2 x 2.1 cm, closely mimicking the size (3.0 x 2.2 cm; Poulin et al. 1996) and color of Common Nighthawk eggs which are creamy white to pale olive gray, usually lightly speckled with grays, browns and blacks (Poulin et al. 1996). We also placed a motion sensitive camera (Bushnell Trophy Cam, Bushnell Outdoor Products, Overland Park, KS, USA) mounted on a low (<0.3 m) tripod. The camera used a highly sensitive infrared motion sensor and recorded predator visits day and night. Cameras were generally

placed 2–4 m from the eggs and were weighted with a brick or rocks to prevent toppling under high wind conditions. Images were time and date-stamped, so timing of predation events was also recorded to the nearest minute.

In Laramie, two-egg clutches were placed on gravel roofs on the University of Wyoming campus. We did not have observations of Common Nighthawks nesting on these roofs, but buildings were chosen based on accessibility, large size, and representation of the range of gravel sizes available as nest substrate. Roofs utilized included Arts and Sciences I (396 m²), II (928 m²), and III (396 m²), and McWhinnie Hall (648 m²). Roofs at Arts and Sciences II and McWhinnie Hall consisted of large gravel or “river stone” (maximum diameter 2.1 cm, range 1.1 – 3.3 cm, $n = 24$), while roofs at Arts and Sciences I and III consisted of smaller pea gravel (maximum diameter mean = 0.7 cm, range 0.3 – 1.1 cm, $n = 24$).

To reduce the possibility that potential predators such as American Crow learned the location of unguarded eggs on urban rooftops, each new set of experimental clutches was placed on a different rooftop, and a rooftop was only revisited after a minimum 7-day interval between trials. In the rural setting at the Spring Creek Preserve, potential experimental nest sites in natural habitats were not limiting, and each clutch was placed in a new location. In all cases, experimental clutches were a minimum of 30 m away from previous trial locations. At both sites, clutches were deployed in late-morning and were monitored for 72 hrs before a nest and camera set-up was removed. A nest was considered depredated if one or both eggs were missing.

We used Excel and on-line worksheets provided by McDonald (2009) to perform statistical tests. We used a *G*-test of independence to test for significant heterogeneity between the proportion of experimental clutches depredated in (a) urban and rural habitats, and (b) urban roofs with small pea gravel compared to those with larger river stone. To assess whether American Crows learned cues to where experimental clutches were placed, we used a Spearman’s rank correlation to test for a significant relationship between the Julian date of experimental clutch initiation and the elapsed time before predation.



FIG. 1. American Crows depredated mock Common Nighthawk nest on pea gravel roof in Laramie, WY. More than 70% of nests in similar habitats were depredated, in contrast to no nests being depredated in natural grasslands in rural areas.

RESULTS

Depredation of experimental nests was significantly more frequent in the urban environment than in the rural, natural habitat ($G = 29.27$, $df = 1$, $P < 0.01$). 44.7% (21 of 47) of experimental nests in the urban environment experienced egg loss, while no nests (0 of 36) were depredated in natural habitats. Depredation was more common at experimental nests on small pea gravel (11 of 15; 73.3%) than on larger river stone (10 of 22; 45.5%), and this difference was significant ($G = 7.48$, $df = 1$, $P < 0.01$).

Predators were identified at 14 nests; in each case the predator was one or more American Crows (Fig. 1). Of the nests depredated, the mean time from deployment to nest loss was 28.0 hrs (range 4.0 – 65.7 hrs, $n = 14$). Six depredate events took place in the early morning (0604 – 0717 hrs), and six occurred in the early evening (1804 – 1917 hrs); the two other depredate events took place at 0946 and 1045. The relationship between the date of clutch initiation and elapsed time before depredate of eggs was not statistically significant (Spearman's $r_s = 0.004$, $df = 12$, $P = 0.99$).

DISCUSSION

Our findings indicate that predation by American Crows on the eggs of Common Nighthawks could occur more frequently in an urban environment than in natural, rural habitats. With 45% of all urban rooftop nests depredated, including 73% of nests on the traditional pea gravel roofs, our

results suggest that crows could limit reproductive success of nighthawks in urban environments. Not all depredate events could be attributed to the American Crow; some predators were missed as a number of experimental clutches (all on urban rooftops) were depredated without photographic images of the predators. Yet of those predation events that were recorded, all were by crows, and it is difficult to imagine anything other than an avian predator being responsible for other losses from rooftops. Rats (*Rattus sp.*), squirrels (*Sciurus sp.*), and raccoons (*Procyon lotor*) may also be suspected of nest losses in urban environments, but none would find easy access to isolated rooftops.

The fact that nearly all (86%) of the identified depredate events took place in the early morning or late evening is consistent with crows being a main predator, and suggests the possibility of regular movements by predatory crows. One possibility is that crows are moving in and out of urban night-time roosts and thus may be responsible for the predation. Although urban roosts are generally associated with winter (Caccamise et al. 1997, McGowan 2001), Marzluff et al. (2001) suggest that urban crow numbers are driven by dispersal from breeding populations in suburban or rural areas where reproductive success is high, and that pre-breeding individuals may make up large flocks in the city where birds have ready availability of rich, anthropogenic food sources. If this is true, then non-breeders may roost within the city even during the breeding season, and this might help explain the observed regularity of predation events captured on camera.

Our study further suggests that rates of predation may vary across different types of gravel roofs. We found significantly higher rates of predation on the small, pea gravel which is traditionally used on urban roofs, but which is declining in popularity as a roofing material (Poulin et al. 1996). The larger, river stone is a more recent advance in roof design apparently preferred for construction because it is less expensive as it does not require the asphalt under-layer needed by the pea gravel (C. Floy, pers. comm.). Because of differences in experimental rates of predation between traditional and more recent roof designs, levels of predation presented here may be seen as conservative; if we had restricted our experimentation only to the more traditional, pea gravel roofs, urban predation rates might be expected to exceed 70%.

The question of why we saw higher rates of predation in urban areas is not resolved by our study. Eggs may be less camouflaged on urban rooftops, especially on the pea gravel where they may stand out against the uniformity of the simple substrate. This may also explain the lower levels of predation of eggs on the river stone where eggs and stone were similarly sized and the substrate slightly more complex due to greater variation in stone sizes. Differences in abundance of crows between urban and rural sites may also play a role in determining predation rates, though we expected at least some predation in rural areas given the common occurrence of crows there.

Whether or not the actual rates of predation on real nighthawk nests in urban settings are as high as we have demonstrated is unknown. Studies using artificial nests have been criticized as being unrepresentative of predation rates from natural nests (Wilcove 1985, Major and Kendal 1996, Zanette 2002, Moore and Robinson 2004). Our study avoided some of the most frequently cited potential biases associated with artificial nest experiments, including differences in experimental and natural nest appearance (Martin 1987), nest height (Ortega et al. 1998), and concealment (Leimgruber et al. 1994), as well as egg color (Yahner and Mahan 1996), egg size (Haskell 1995), and human visitation rates (Major 1990). Perhaps more likely contributions to potential bias in our data is the absence of parental defense activity at mock nests (Rudnicki and Hunter 1993), and human scents on the eggs (Sloan et al. 1998), and these factors could contribute to an elevated predation rate.

Regardless of whether or not actual rates of predation on nighthawk nests in urban settings are as high as we have demonstrated, we assume that the *relative* difference that we found in predation between urban rooftop nests and rural nests is real. Our finding of no predation on eggs in natural habitats may be representative, as predation on Common Nighthawk nests in native grasslands is reported to be quite low (Poulin et al. 1996, Allen and Peters 2012). Thus, if our study successfully represents relative predation pressure at nests on urban rooftops as well as it apparently does at nests in native grasslands, then predation rates at urban rooftop nests may indeed be as high as encountered in our experimental study.

Nevertheless, we do need a better indication of how predation in urban areas affects nighthawk population trends. Our results suggest that urban

areas could be an ecological trap (Dwernychuk and Boag 1972) in that nighthawks may be selecting rooftop nesting substrates that appear suitable but then experience extremely high rates of nest loss to predators. Knowing to what degree nighthawks actually select rooftop nest sites (Brigham 1989, Poulin et al. 1996), or how this behavior may vary geographically (Brigham 1989), would be informative. In addition, data related to the decline in pea gravel roofs and whether the loss of this nesting substrate might force birds into even poorer quality urban rooftops, or alternatively, might benefit the species by eliminating a potential ecological trap, is also required. But studying natural nests is preferred to gain a fuller understanding of predator pressure on Common Nighthawks. Locating natural nighthawk nests is surely time-consuming and difficult, yet it has been shown to be possible in some natural settings (Allen and Peters 2012). Given our results with artificial nests, additional studies targeting predation of natural eggs and nestlings, and measures of reproductive success, should be a priority and will be useful for more fully assessing factors responsible for nighthawk population declines and informing conservation planning.

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