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Resolving the urban nest predator paradox: The role of alternative foods for nest predators

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ABSTRACT

Urbanization is a leading cause of species endangerment in the United States; however, certain species thrive in urban habitats. The loss of key predators or the addition of new predators in urban areas could alter the structure of urban communities. A reduction in nest predation is hypothesized to explain the high density of urban birds, yet urban areas typically have increased populations of avian nest predators. The loss of important nest predators in urban habitats, prey switching of urban predators, or successful nest defense against avian nest predators could explain this urban nest predator paradox. To assess these hypotheses I compared nest predation rates of Northern mockingbirds (*Mimus polyglottos*) in parking lots and residential neighborhoods to populations in pastures and wildlife preserves during 2007–2009 in Florida, USA and placed video cameras on a subset of nests in 2008–2009. Data do not support the hypothesis that urban nest predation rates are consistently lower than non-urban nest predation rates. Of the 56 nest predation events recorded, cats were the dominant urban predator and Cooper's hawks (*Accipiter cooperii*) were the dominant non-urban predator. There was no evidence for a loss of important nest predators in urban habitats; however, prey switching by Cooper's hawks likely occurred. There was also indirect evidence for the importance of nest defense. Furthermore, some of the cats recorded as nest predators in residential neighborhoods were owned cats and all but one cat predation event occurred at night. To reduce nest predation rates, cat owners should keep their cats indoors at night.

1. Introduction

The amount of land area being converted to urban land-use is rapidly increasing and by 2050, the United Nations estimates that the global urban population will equal ~6.5 billion (United Nations, 2006). Urbanization is one of the leading causes of species endangerment in the United States (Czech and Krausman, 1997) and although many native species are extirpated from urban areas, some seemingly adapt well (Blair, 1996; Shochat et al., 2006). Species that are more abundant in urban settings have been referred to as urban exploiters (commensals of humans) and urban adapters (native species that maintain urban populations), while species that are less abundant or absent from urban areas have been termed urban avoiders (Blair, 1996; Shochat et al., 2006). These terms, however, do not simply describe relative abundances of species, but also imply processes that determine the abundance of these species in relation to urbanization. For the vast majority of species, however, we do not yet know the processes that are driving their observed abundance in urban habitats. For example, the term urban avoiders implies a behavioral response to urbanization whereby individual birds choose not to settle in urban habitats. While this may be the case for many species, other species may have attempted to settle in urban habitats and failed. I therefore suggest the following process-neutral terms that simply reflect the relative abundances of species in different habitats. Human commensals are species that only occur in human-dominated habitats. Urban-positive species are more abundant in urban habitats than non-urban habitats. Urban-neutral species are equally abundant in urban and non-urban areas, while urban-negative species are more abundant in non-urban than urban habitats. Urban-absent species are only found in non-urban settings.

Populations of urban-positive species that reside in towns and cities can form a significant proportion of the global population of these species (Mason, 2003; Bland et al., 2004; Chamberlain et al., 2009; Fuller et al., 2009). Understanding the factors that promote the success of urban-positive species is necessary if we are to gain a complete understanding of the processes that shape urban wildlife communities and provide meaningful recommendations to urban planners and concerned citizens that will allow us to retain or even enhance urban wildlife communities.

The predator refuge hypothesis (Gering and Blair, 1999; Shochat et al., 2004, 2006; Faeth et al., 2005; Chamberlain et al.,

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2009) proposes that the success of urban bird species is the result of a reduction in nest predation rates in urban habitats. Evidence for this hypothesis is mixed. Some studies have documented reduced rates of urban nest predation (e.g., Gering and Blair, 1999; Kosinski, 2001), whereas others have documented increased urban nest predation rates (e.g., Jokimaki and Huhta, 2000; Thorington and Bowman, 2003) or no differences (e.g., Melampy et al., 1999; Haskell et al., 2001; Reidy et al., 2008; Rodewald and Shustack, 2008). Thus, the general applicability of the predator refuge hypothesis as an explanation for the success of urban-positive species is far from clear. Our ability to interpret these conflicting results is hampered by our lack of knowledge about (1) how different potential nest predator populations respond to urbanization and (2) the relative importance of these different potential predators in determining nest predation rates.

One possible explanation for reduced urban nest predation rates is that there are simply fewer nest predators in urban areas. In general, research has demonstrated increased nest predation rates with increasing predator abundance and/or activity (e.g., Andrén, 1992; Zanette and Jenkins, 2000; Schmidt and Ostfeld, 2003; Cain et al., 2006; Sperry et al., 2008); therefore if there are fewer predators in urban habitats, then there should be reduced nest predation rates. Although we lack data on how most groups of nest predators respond to urbanization (Stracey and Robinson, in press), the abundance of at least some nest predators is actually higher in urban habitats. For example, many avian nest predators (Gregory and Marchant, 1996; Jokimaki and Huhta, 2000; Marzluff et al., 2001; Sorace, 2002; Sorace and Gustin, 2009; Rodewald et al., in press), raccoons (Prange et al., 2003; Randa and Yunger, 2006; Rodewald et al., in press), and cats (Sorace, 2002; Rodewald et al., in press) are consistently more abundant in urban than in non-urban habitats. This mismatch between predation rates, which are often lower in urban areas, and predator abundance, which is often higher in urban areas, has been termed the "urban nest predator paradox" (Shochat et al., 2006; Stracey and Robinson, in press).

While we can generate a laundry list of species that have been documented as nest predators, in most cases the species included are based upon anecdotal eyewitness accounts of predation events and not on systematic studies of nest predator identity. Not all predators are created equal: certain species likely only infrequently depredate nests, whereas other species are consistently important nest predators (Schmidt et al., 2001). If important nest predators are replaced with species that only occasionally depredate bird nests (weak predators), then the absolute abundance of potential nest predators may not be a good predictor of actual predation rates (Haskell et al., 2001; Marzluff et al., 2001; Schmidt et al., 2001). Instead, predation rates may reflect the abundance of a few strong predators (species that are responsible for the majority of predation events and thus drive rates of nest predation; sensu Schmidt et al., 2001). I define the strong predator abundance hypothesis as the loss of strong predators in urban habitats leading to a reduction in nest predation rates. Until we know more about the actual identity of the predators that attack nests and on how this varies between urban and non-urban habitats, we cannot evaluate this hypothesis.

Alternatively, whether or not a species acts as a strong nest predator could be context-dependent (Navarrete and Menge, 1996). If urban predators undergo prey switching (e.g., Miller et al., 2006; Randa et al., 2009; Rodewald et al., in press), then predation rates on urban bird nests might be reduced and otherwise strong predators may become weak predators in urban environments. I term this the urban prey switching hypothesis. Urban habitats are characterized by abundant anthropogenic food that can subsidize generalist nest predators (Prange et al., 2004; Marzluff and Neatherlin, 2006; Whithey and Marzluff, 2009). Prey switching may therefore result in reduced nest predation rates despite abundant nest predators (Schmidt, 1999; Miller et al., 2006). Indeed, Rodewald et al. (in press) found that predation rates were correlated with predator abundance in rural areas, but were not correlated in urban habitats.

An additional factor that must be considered in studies of nest predation in urban communities is nest defense behavior, both in terms of nest placement and predator mobbing. Active nest defense can be an effective means of decreasing rates of nest predation (reviewed in Martin, 1992). Some species may be able to persist or even thrive in the face of high predator populations because they are able to defend their nests effectively against the dominant predators in a habitat (the predator defense hypothesis: Stracey and Robinson, in press). Mobbing may be especially effective in urban areas because many of the numerically dominant predators are birds such as crows and blackbirds that can potentially be chased away by aggressively mobbing parents.

Before we can test these hypotheses, we need data on which of the many potential predators are responsible for the majority of nest predation events and on how the identity of predators differs in urban and rural communities. Reidy et al. (2008) found no differences between urban and non-urban habitats in nest predation rates or in predator identity. This comparison, however, was made between patches of natural vegetation surrounded by either residential development or by rural areas. In this study I attempt to resolve the urban nest predator paradox for one urban-positive species, the Northern mockingbird (*Mimus polyglottos*), by using video cameras to compare the identity of nest predators at nests in the urban matrix and non-urban habitats. Data on mockingbirds from 2005–2006 support the hypothesis that urban nest predation rates are lower than non-urban nest predation rates (Stracey and Robinson, in press), yet many potential avian nest predators (fish crow, common grackle, boat-tailed grackle) are more abundant in urban habitats in North Florida (Stracey and Robinson, in press). The urban nest predator paradox (e.g., lower rates of nest predation in urban habitats that have more abundant nest predators) assumes that there is a tight correlation between nest predation rates and predator abundance. This assumption, however, may not reflect, (1) prey switching and (2) the disproportionate effect of a few strong, but less abundant, predators. In both cases, the most abundant avian nest predators in urban habitats would account for relatively few predation events. If prey switching drives the urban predator paradox, then I would expect to see higher relative rates of predation in non-urban habitats by predators that are common to both habitats. If the predator paradox can be explained by the strong predator abundance hypothesis, then I predict that the dominant non-urban predators would be uncommon in urban habitats. Future research on the diet of urban predators and the abundance in urban areas of the dominant non-urban predators will be necessary to further test both of these hypotheses.

2. Methods

2.1. Nest predation rates

I collected data on nest predation rates at seven study sites (two parking lots, three residential neighborhoods, two pastures, and one wildlife preserve) in areas in and around Gainesville, FL between February and August of 2007–2008 (Stracey, 2010). In 2009, I did not collect data from one of the residential neighborhoods, one of the parking lots, and one of the pastures. I located nests and checked their contents every one to 4 days. For each year I calculated habitat specific nest survival rates and 95% confidence limits using the logistic exposure method (Shaffer, 2004, SAS 9.1). Because I was interested in predation rates, I only considered nests